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Breeding and Improvement *of* Farm Animals

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With Chapter on

Selection in Meat Animals

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FOURTH EDITION

NEW YORK TORONTO LONDON
McGRAW-HILL BOOK COMPANY, INC.
1951

McGRAW-HILL PUBLICATIONS IN THE AGRICULTURAL SCIENCES

R. A. Brink, *Consulting Editor*

17

BREEDING AND IMPROVEMENT OF FARM ANIMALS

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BREEDING AND IMPROVEMENT OF FARM ANIMALS

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THE MAPLE PRESS COMPANY, YORK, PA.

PREFACE TO THE FOURTH EDITION

In the Preface to the First Edition, published in 1926, we said, "This book has been written primarily for use as a textbook of animal breeding. It treats the subject of breeding practice from the scientific standpoint in so far as this is possible at the present time. Breeding is an art to be learned only by practice, but knowledge of principles supplies the only firm foundation for its practice. Superior animals will be more numerous when breeders know why as well as how."

Part of the Preface to the Second Edition, published in 1934, reads, "Great progress has been made in all three of the fields included in the scope of this book since its publication in 1926. In the field of *reproductive physiology* significant discoveries have been made in matters pertaining to the endocrine control of sex manifestations as well as in those dealing with the maintenance of genital health and normal activity. Great forward strides have been made also in the science of *genetics* and new phases of this subject have been developed. These include among others the artificial induction of mutations by radiation or heat; the development of the theory of genic balance; and the cytological demonstration of crossing over. The mechanism of transmission is now pretty thoroughly understood and the chromosomal interpretation of inheritance established beyond reasonable doubt. Of great significance, also, are the new approaches and points of view that have come to the fore in the *art of breeding*. Rules of thumb are fast passing into the discard and breeders are now basing their operations on sound physiological and genetic principles."

The Preface to the Third Edition, published in 1942, is included in full on the following pages.

In the present revision, the basic organization remains as it has been from the start, *viz.*, (1) a general introductory section, followed by sections dealing with (2) reproductive physiology, (3) genetics, and (4) selection. During the past eight years, significant advances have been made in all these fields: a broadened recognition of the fundamental aspects of animal agriculture together with breed advancements, and shifting emphasis among the various classes of livestock as indicated in Section I, Animals and Man Up to the Present; further unraveling of the intricate interactions of the hormonal regulation of sex manifestations and the widespread use of artificial insemination as portrayed in Section

II, Mechanisms of Reproduction; continuing delineation and refinement of the basic laws of inheritance and their application to livestock improvement as shown in Section III, Mechanisms of Heredity; and a concerted experimental attack on the problems and implications of the various systems of breeding as related to the main function of animal breeding—more successful selection as demonstrated in Section IV, The Art of Breeding.

For ultimate success in creating more efficient and beautiful animals, one must possess an understanding of the basic principles underlying reproductive physiology and inheritance and then gather, interpret, and apply performance facts about his animals so that the hereditary determiners for desirable qualities may slowly but surely replace those for undesirable qualities now present in the germ cells of the animals currently constituting his herd or flock.

It is the authors' hope that this book may provide both the knowledge and the inspiration to accomplish this most worth-while and interesting task.

We are again indebted to many friends, authors, and publishers for kindly criticisms, helpful suggestions, and permission to quote and to reproduce illustrative materials. We are happy to acknowledge our special indebtedness for helpful suggestions to Doctors B. B. Bohren and A. E. Bell and Professor R. B. Cooley of Purdue University; Dr. W. A. Craft of the Regional Swine Breeding Laboratory; Doctors J. E. Nordby and C. E. Terrill of the Regional Sheep Breeding Laboratory; and to Professor W. A. Cowan of the University of Massachusetts.

Our very deep appreciation is hereby extended to Dr. E. J. Warwick for his generous and penetrating suggestions throughout our labors and for his willingness to contribute the chapter on selection in meat animals.

For invaluable clerical assistance, we wish to thank Mrs. G. R. Ruddeforth and Mrs. W. A. Cowan of Amherst, Massachusetts, and Mrs. Thelma Boesch of Lafayette, Indiana.

We shall always welcome constructive criticism.

VICTOR ARTHUR RICE
FREDERICK NEWCOMB ANDREWS

AMHERST, MASS.
LAFAYETTE, IND.
October, 1950

PREFACE TO THE THIRD EDITION

In the early history of the Land Grant Colleges there was an almost complete lack of technical agricultural science supported by experimental data, with the result that curriculums were built largely out of liberal arts materials. Today we have reached the other extreme with so much well-supported technical agricultural science data available that the student of agriculture has all too little time for liberal or cultural courses. Most agricultural students probably get a smattering of reproductive physiology in general courses in anatomy and physiology and a smattering of genetics in general courses in biology; but since the limitations of time so often prevent the inclusion of separate courses in reproductive physiology, animal hygiene, genetics, embryology, etc., and since the inclusion of all these courses would exclude just so many more cultural courses, the author has proceeded on the basis that undergraduate students in animal husbandry should have one complete course in animal breeding with reproductive physiology, genetics, and the art of breeding brought together into one complete whole. He has also endeavored to make this something more than just a technical book on breeding by giving a bit of the historical background involved and by indicating some of the broader implications of the place of man and his animals on this planet; but he has tried to leave to the reader the matter of drawing philosophical deductions.

This book is comprised of four sections. Section I begins with the present status of animal breeding and then traces it back to its probable beginnings. The origins of both man and his animals are investigated, as well as the broader aspects of the evolutionary process that apparently brought both into existence.

Section II deals with the processes involved in the physiology of reproduction both from the scientific and the practical angle. The breeder should be acquainted with the normal functioning of the genital systems in order that his herds and flocks may be maintained at a high level of reproductive efficiency.

Section III is devoted to a study of the principles of heredity. The various types of behavior of the chromosomes and genes, passed on to each new individual by means of the germ cells of its parents, in the perpetuation of ancestral traits or the creation of variations from the older patterns, are considered in some detail. Although the direct manifestations of many of these principles which are explicitly detailed

in lower organisms are difficult or impossible of exemplification in the higher species, it is a virtual certainty that they are at work. Therefore a full understanding of the basic principles is necessary if the breeder is to handle, in the most intelligent and profitable manner, his practical problems of selection.

Section IV is devoted to what is often called the *art of breeding*, which may be summed up in one word *selection*. This term has both a present and a future connotation, since a breeder is constantly selecting from among the best animals making up his herd or flock on the basis of their pedigrees and performance, and he is also anticipating future selection by planning matings to create new animals of a preconceived pattern. Selection, therefore, involves the various systems of breeding both among related and unrelated individuals. In the final chapter the reader can glance backward over the trail that animal breeders and scientists have blazed and look forward to try to foresee "the shape of things to come."

It is the author's hope that this book will be stimulating and helpful to students of breeding both in classrooms and on livestock farms.

Many friends have assisted the author in the preparation of this book; among them Drs. H. H. Plough and Charles L. Sherman of Amherst College; Dr. Harry L. Shapiro of the American Museum of Natural History, New York; Mr. Bradford Knapp, Jr., of the Bureau of Animal Industry, Washington, D.C.; and Drs. G. Chester Crampton, John B. Lentz, Frank H. Hays and Mr. Floyd Johnson of the Massachusetts State College. Special thanks are due Dr. F. N. Andrews of Purdue University, Dr. Arthur B. Chapman of the University of Wisconsin, and Drs. Hugh C. McPhee, Ralph W. Phillips, and Ralph G. Schott of the Bureau of Animal Industry, Washington, D.C., for their suggestions and constructive criticisms. The author is also greatly indebted to Mr. Talcott Edminister for assistance in reading proof, and to Miss Evelyn Day, who in some ingenious manner deciphered the original manuscript and put it through a typewriter.

The author is indebted to Prof. R. A. Fisher and to Messrs. Oliver & Boyd, of Edinburgh, for permission to reprint Tables 29 and 31 from their book *Statistical Methods for Research Workers*, 8th edition (1941).

Grateful acknowledgment is also made to various authors and publishers for permission to use certain of their materials.

If the reader is curious as to the sources of the ideas herein expressed, he may discover them in great measure through consulting the references listed at the close of each chapter.

VICTOR ARTHUR RICE

AMHERST, MASS.
March, 1942

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To

All Who Love Fine Animals

An artist, modeling in plastic clay or conjuring with marble, brings forth a conception that the world acclaims a triumph. He deals, however, with his materials direct, and they respond instantly to his slightest touch, as he toils toward a preconceived ideal. There is no resistance to his manipulations.

What, then, should be our estimate of the work of one who has first to conceive the figure in his brain; whose only tools are the laws of heredity, selection, inbreeding, outcrossing, and alimentation; whose only materials are flesh and blood, unapproachable except by indirection; who battles ever against the stubborn forces of atavism or reversion to ancestral forms; who seeks, and succeeds in producing, a creature pulsating with life, exquisitely fashioned, down to the minutest detail, not only a thing of beauty in itself—which artists try, sometimes with ill success, to reproduce on canvas or in bronze—but a creation that serves as well the highest utilitarian purpose?

The breeder of animals (or plants) directs the spark of life itself. The possibilities of his art are almost infinite.—A. H. SANDERS.

THE NATIONAL GEOGRAPHIC MAGAZINE
December, 1925

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SECTION I

Animals and Man Up to the Present

CHAPTER I

ANIMAL BREEDING—PRESENT AND PAST

Successful animal breeding depends primarily on the proper choice of parents for the next generation. The A, B, C's of it are, therefore, Ancestors Better Chosen. Since any farm animal arises from the union of one egg and one sperm, we can epitomize the whole problem by saying that whenever better eggs are fertilized by better sperm, we will have better animals—and there is absolutely no other way to get them. So, it is apparent that the breeder's task is that of ascertaining as precisely as possible what the germ cells of his animals contain in the way of hereditary determiners of potentialities for the next generation. To know the details of the workings of the reproductive organs as they perform their two functions of (1) bridging the gap between the generations and (2) setting up the specifications for the next generation is quite obviously the breeder's first task. Fortified with this basic knowledge, he can then tackle his second job of dovetailing systems of breeding and selection into a more efficient tool for creating improved livestock.

Animal breeding is one of the largest industries in the United States. The total national income in 1950 was 235.6 billion dollars. Farm income was 27.9 billion, and of this, 15.5 billion was income from livestock and livestock products. Animals of some type are to be found on about 90 per cent of our farms in the United States. Livestock breeding involves nearly 200 million farm mammals, 700 million poultry and other birds, in addition to an innumerable host of dogs, cats, white rats; also foxes, ferrets, and other fur bearers, not to mention among others guinea pigs, guppies, and goldfish. Animal breeding for some is a hobby, but many thousands of people depend upon it for their livelihood. In terms of food, clothing, and the maintenance of soil fertility, every person in the United States has a stake in its success.

Hobbyist and realist are trying in most instances to shape the external form of their animals according to some preconceived plan and at the same time to include within this desirable exterior form some combination of mental and physiological characters that will have a high commercial or

aesthetic value. The horseman wants speed and stamina; power, patience, and persistence; easy gait and companionability. The cattleman wants a compact animal that will fatten rapidly into a carcass of good quality; the dairyman wants a "typy" cow that will yield a large

TABLE 1.—NUMBER AND AVERAGE VALUE PER HEAD OF THE VARIOUS CLASSES OF FARM LIVESTOCK IN THE UNITED STATES, 1880–1950

Year	Horses on farms		Mules on farms		Dairy cattle	
	Number (000 omitted)	Av. value	Number (000 omitted)	Av. value	Number (000 omitted)	Av. value
1880	10,903	$ 53.74	1,878	$ 61.74	11,754	$ 23.31
1890	15,732	69.27	2,322	77.61	15,000	22.30
1900	17,856	43.56	3,139	51.46	16,544	31.30
1910	19,972	107.70	4,239	119.98	19,450	35.40
1920	20,091	96.45	5,651	148.29	21,455	81.51
1930	13,742	69.98	5,382	83.93	23,032	82.70
1940	10,616	77.43	4,321	114.53	25,334	57.22
1950	4,763	43.30	1,990	82.00	24,579	218.00

Year	Cattle other than milk cows		Sheep		Hogs including pigs	
	Number (000 omitted)	Av. value	Number (000 omitted)	Av. value	Number (000 omitted)	Av. value
1880	31,593	$ 15.75	44,867	$ 2.18	44,327	$ 4.40
1890	45,014	15.16	42,693	2.29	48,130	4.80
1900	43,195	24.67	45,065	2.97	51,055	5.36
1910	39,543	19.20	46,939	4.06	48,072	9.05
1920	48,945	39.99	37,328	10.59	60,159	20.00
1930	39,971	40.38	45,477	9.00	55,705	13.45
1940	43,435	30.86	48,473	6.33	58,312	7.79
1950	59,600	136.00	28,065	26.40	65,028	38.20

amount of milk of a high quality over a lengthy period. The sheepman wants quality and quantity in both carcass and wool; the hog man as much high-quality pork as he can get from each sow in his herd each year. The dog fancier wants looks, smartness, companionability, and sometimes utility. All of them want docility, longevity, freedom from disease, regularity of breeding, etc.

Can these various combinations be had in single animals? The answer

obviously is "yes" because we have had such animals in the past and have some of them today. Can we so breed our animals that they not only will have these desirable combinations of qualities but also will be able to pass them on to their offspring? The procedure for accomplishing the latter purpose is now known, and the purpose of this book will be to demonstrate the principles underlying reproduction, hereditary transmission, and variation and to show how selection involving the various systems of breeding can be made to yield certain definite results.

Livestock Trends in the United States.—In Table 1 will be found an enumeration of the various farm mammals over the past 70 years. It is obvious from Table 1 that mechanical power has rapidly been supplanting horse and mule power since 1920. Whether machines will entirely sup-

TABLE 2.—TOTAL NUMBERS AND VALUE OF FARM MAMMALS AND HUMAN POPULATION, UNITED STATES, 1880–1950*

Year	No. of all farm livestock	Value of all farm livestock	Human population, United States†
1880	120,990,000	$ 1,576,636,520	50,156,000
1890	165,286,000	2,418,774,100	62,948,000
1900	170,315,000	2,581,751,910	75,994,000
1910	178,355,000	4,649,803,510	91,972,000
1920	196,875,000	7,383,500,260	105,711,000
1930	185,464,000	5,995,084,680	122,775,000
1940	196,491,000	4,904,307,000	131,669,000
1950	184,025,000	16,712,631,000	153,000,000‡

* Horses, mules, cattle, sheep, swine.
† To even thousands.
‡ Estimate.

plant horses and mules as power units, the future will tell. Only from one-fourth to one-half as many work horses and mules are being produced as would be needed to maintain their numbers. On the other hand, there seems to be a growing interest in the horse for pleasure purposes. Dairy-cattle numbers have shown a steady increase over the last 70 years. Meat animals have had a slight actual increase and, in addition, they now mature more rapidly than formerly, the quicker turnover actually meaning more product from a given number of animals. Many factors, of course, influence the numbers of animals kept on farms from year to year. The magnitude of the total value of American livestock and the meagerness of the average value stand in marked contrast to each other. Both of these points indicate opportunity for the livestock breeder.

Table 2 shows the trend in total numbers and total value of farm livestock in the United States by decades for the past 70 years and the trend

in human population. It shows that the breeding of livestock is one of the most important types of endeavor in this country.

TABLE 3.—AUCTION-SALE PRICES OF PUREBRED CATTLE

Breed	1920	1924	1928	1932	1936	1940	1944	1948
Ayrshire	$359	$124	$184	$108	$156	$146	$196	$321
Guernsey	508	380	334	162	252	225	358	415
Holstein	372	192	218	105	164	173	327	439
Jersey	354	206	211	126	161	147	251	373
Aberdeen-Angus	705	150	170	106	161	209	336	533
Hereford	416	133	210	105	151	195	317	497
Shorthorn	603	160	192	104	137	171		

TABLE 4.—MILK AND FAT PRODUCTION OF PURE BREEDS*

Breed	No. of records	Av. No. of days	Av. pounds of milk	Av. pounds of fat
Holstein (AR)	60,375	315	16,440	570.0
Holstein (HIT)	220,195	....	11,213	391.4
Brown Swiss (ROP)	1,329	305 2×	10,341.57	424.63
Brown Swiss (ROP)	591	305 3×	11,901.93	483.75
Brown Swiss (ROP)	897	365 2×	11,626.02	474.35
Brown Swiss (ROP)	1,337	365 3×	13,752.34	551.85
Brown Swiss (HIR)	14,132	305 2×	9,159.78	362.84
Brown Swiss (HIR)	999	305 3×	11,653.4	464.88
Guernsey	22,361	365	11,014	541
Guernsey†	3,351	305 3×	9,723	470
Guernsey†	17,420	305 2×	8,036	390
Guernsey (HIR)	50,240	....	8,159	396
Dutch Belted	100	365	10,844.32	414.09
Devon	46	365	7,484.4	339.99
Red Poll	1,915	....	8,692.88	373.88
Jersey (HIR)	22,385	....	7,070	374
Ayrshire‡	10,118	....	9,846	401
Milking Shorthorn	22,580	348	8,972	357.08
American Dairy Cattle Club	1,985	305	10,584	437

* New England Homestead, Springfield, Mass., Sept. 24, 1949.

† Carried calf 175 days or more of record. Guernsey AR averages of records completed during last 5 years.

‡ Ayrshire Association has discontinued computing records on a herd-test yearly basis. Their practice now is to compute a new average each year.

Value of Purebred Animals.—Table 1 shows the low value of the average animal in each class. Now let us look at the brighter, upper side of the picture. Table 3, for example, gives some auction-sale prices of purebred cattle.

On the average the monetary value of purebreds always exceeds that of grade animals. It is sometimes argued that grades are practically as good as purebreds, and the fact that the grades generally owe their desirable qualities to the "blood" of registered animals is entirely overlooked. In commercial production, grade animals will probably always fill a very important place, but they will probably continue to depend on the purebred for their improvement, although this is not necessarily so. Actually, less than 5 per cent of the animals in any class are purebred and registered. The great bulk of our animals are unregistered purebreds or grades. The purebred breeder, therefore, faces a great and continuing challenge in planning his breeding operations so that he will be producing sires which are capable of improving grade herds. The practice of artificial breeding, now gaining so rapidly in dairy-cattle operations, should be a great boon to the commercial producer, since if properly organized and administered, it should remove one of the stumbling blocks to his progress, namely, that of securing better sires.

Table 4 gives some production figures for the various breeds of dairy cattle.

Still another aspect of the possible rewards in the purebred business is shown by the following tabulation of some auction-sale record prices for livestock.

All-time Auction Records[1]

Aberdeen-Angus—male, Prince Eric of Sunbeam, $40,000; female, Erianna B. 6th, $25,000.

Ayrshire—male, Netherhall Swanky Dan, $20,000; female, Low Milton Queen of Hearts, $10,277.

Brown Swiss—male, Colonel Harry of Judd's Bridge, $23,500; female, James Chloe of Judd's Bridge, $11,500.

Guernsey—male, Gardenville Coronation King, $45,000; female, Shuttlewick Levity, $25,000.

Hereford—male, WHR Helmsman 89th, $61,000; female, WHR Lady Lill 15th, 3769212, $20,000.

Holstein-Friesian—male, Prince Aggie of Berylwood, $110,000; female, Pabst Korndyke Cornflower, $30,000.

Jersey—male, Sybil's Gamboge, $65,000; female, Wonderful Dreaming Givia, $21,000.

Polled Hereford—male, AFL Choice Domino 6th, $35,000; female, Trumain Domino 63rd, $10,000.

Red Poll—male, Billy Charmer, $2,000; female, Dandy Lou, $1160.

Shorthorn—male, Pittodrie Upright, $61,335; female, 8th Duchess of Geneva, $40,600.

Belgian—male, Farceur, $47,500.

[1] *New England Homestead*, Springfield, Mass., Sept. 25, 1948, p. 30.

Clydesdale—male, Baron of Bucklyvie, $47,500.
Percheron—male, Philix, $9000; female, Iolanthe, $3500.
Suffolk—American sales, Boxted Confider, $3,700; female, Rose Mary, $1,225.

As shown in Table 5, most of our purebred breed associations in the United States were formed about 1875–1885. Importations of purebred livestock into this country preceded this, to be sure, but improved breeding was given great impetus by the formation of the breed associations. Table 5 also shows the number of animals of the different breeds that have been registered up to the present.

Some people maintain that our primary problem in animal husbandry is not that of better breeding but rather one of better feeding and management. Several experiment stations have purchased cows with records from dairymen and increased their production by 2,000 or 3,000 lb. as a result of better feeding and management. The average cow produces about 5,000 lb. of milk yearly. Is her actual inheritance 7,000 or 8,000 lb.? Could be, but is it? Disease also takes its toll in all our classes of livestock. Studies show that about 50 per cent of the dairy cows which leave herds annually do so because of low production and disease. Early death, failure to grow rapidly, thus delaying first calving in dairy cattle and arrival at market in fat stock, too long intervals between parturitions, too high a percentage of herd replacements yearly, and low production or rate of growth through poor feeding and management cost animal agriculture untold millions yearly. Of 100 pigs born, about 56 eventually get to market. This little pig went to market, this little pig stayed home—period. Certainly there is great need for better feeding and management—"half the breeding goes down the throat." But all this being true does not in any way lessen the need for better breeding in terms of production, type, longevity, resistance to disease, regularity of breeding, etc.

Foods of Animal Origin.—A rapidly increasing population does not necessarily mean the extinction of any particular class of livestock. It should, however, mean the rapid passing of inefficient members of all classes. Thickly populated European countries still produce meat, milk, wool, and power. The actual number of animals in the United States, together with their increasing productivity, mean that our population is consuming an increasing amount of animal products. The population of the United States was about 5 million in 1800 and has grown to about 147 million in 1949. It has been variously estimated that the total population that can be provided with home-grown food in the United States is 200 up to 331 million. This is based on maintaining the present dietary standard. The average per capita consumption of dairy products is still far below the nutritional optimum, for our people consume on the average

TABLE 5.—NUMBER OF REGISTRATIONS IN THE VARIOUS PURE BREEDS*

Breed	Membership	1948 registrations	All-time registrations
Cattle Associations			
Hereford	16,000	352,888	5,825,000
Holstein	39,516	168,338	4,154,304
Shorthorn	23,842	49,674	3,170,463
Jersey	3,445	66,766	2,233,025
Guernsey	3,693	96,895	1,616,326
Aberdeen-Angus	15,000	84,078	1,158,372
Ayrshire	7,733	26,113	492,459
Polled Hereford	7,000	34,110	356,732
Brown Swiss	2,568	22,625	296,396
Polled Shorthorn	2,447	10,326	223,935
Milking Shorthorn	7,890	24,650	200,000
Red Poll	3,000	4,274	181,942
Brahman	992	15,145	109,917
American Galloway	24	648	51,701
Devon	75	365	32,590
American Dairy Cattle	200	2,000	19,000
Dutch Belted	35	50	7,377
Red Danish	155	10	3,500
American Scotch Highland	16	434	434
Kerry and Dexter	No report 40 (1948)	....	150
Sheep Associations			
Shropshire	12,160	16,523	1,117,000
Hampshire	6,400	28,390	880,482
Rambouillet	2,054	9,704	514,136
Oxford	1,450	3,179	193,950
Southdown	1,234	8,172	192,033
Cotswold	1,100	375	126,366
Corriedale	1,320	10,904	92,669
Dorset	500	3,487	79,135
Lincoln	No report 135 (1948)	764	68,132 (1948)
Cheviot	About 700	2,345	55,000
Texas Delaine-Merino	188	2,120	41,478
American Suffolk	344	5,921	41,412
Columbia	288	3,390	28,990
Romney	200	1,608	28,608
National Suffolk	300	3,750	26,055
Karakul	491	1,005	19,275
Black Top-National	24	110	1,081
Delaine-Merino			
American and Delaine-Merino	No report		

TABLE 5.—NUMBER OF REGISTRATIONS IN THE VARIOUS PURE BREEDS.*—(*Continued*)

Breed	Membership	1948 registrations	All-time registrations
Horse Associations			
Percheron	6,500	251	247,893
Thoroughbred	50	8,375	108,375
Saddle	500	4,477	79,477
Belgian	4,450	350	62,739
Jack and Jennet	2,200	66	37,028
Tennessee Walking	1,056	3,319	33,642
United States Trotting	7,500	3,536	27,323 (since 1938)
Shetland Pony	681	849	26,111
Clydesdale	130	45	25,460
Shire	1,100	16	21,959
American Quarter	4,500	3,849	17,895
Morgan	500	469	17,751
National Quarter	Over 3,000	3,041	13,833
Palomino (Texas)	3,000	1,000	8,071
Palomino (California)	600	685	5,420
Suffolk	120	9	
Arabian	650	600	5,200
Morocco Spotted	500 active	94	1,390
Welsh Pony	30	46	1,260
Albino	150	73	900
Appaloosa	204	314	850
Pinto	No report 535 (1948)	95	625 (1948)
Swine Associations			
United Duroc	6,760	100,391	2,603,068
Poland-China	11,400	30,800	2,208,637
Hampshire	9,000	50,217	776,875
Chester White	3,782	23,861	699,694
Berkshire	11,500	24,000	635,317
National Spotted Poland-China	12,995	48,216	625,061
O.I.C	1,176	16,254	270,024
National Hereford	2,041	9,200	80,833
Yorkshire	800	5,912	61,890
Chester White Record	2,363	2,332	29,916
Essex	90	200	14,765 (1948)
Inbred Livestock	551	3,890	10,427
National Mule Foot	150		
Kentucky Red Berkshire	15	112	2,352
Tamworth	80	1,400	1,533
Goat Associations			
American Angora	624	7,156	232,000
American Milk Goat	1,700	4,036	93,387
†American Goat	1,000	3,550	35,000
Rabbit and Cavy Associations			
American Rabbit and Cavy Breeders	8,745	20,201	47,894

* New England Homestead, Springfield, Mass., Sept. 24, 1949.
† Purebreds. AGS does not register grades.

about 2.2 glasses of milk; ½ oz. of butter (2 pats), ⅓ oz. of cheese per person per day, and about 2 dishes of ice cream per person per week. In addition, there is an average consumption of about 1 can of evaporated milk per person every 3 weeks, plus a small amount of sweetened condensed milk.

The 1948 per capita consumption of meat was as follows: beef, 63.4 lb.; veal, 9.4 lb.; lamb, 5.0 lb.; pork products, 68.3 lb.; a total of 146 lb. per capita per year. This is lower than it is in several countries, higher than that in many other countries. Whether or not it is the optimum, the writer does not know, but he is confident that meat would be in greater demand if the means for its purchase could be made available. In terms of the 21 meals that most of us eat each week, our present consumption

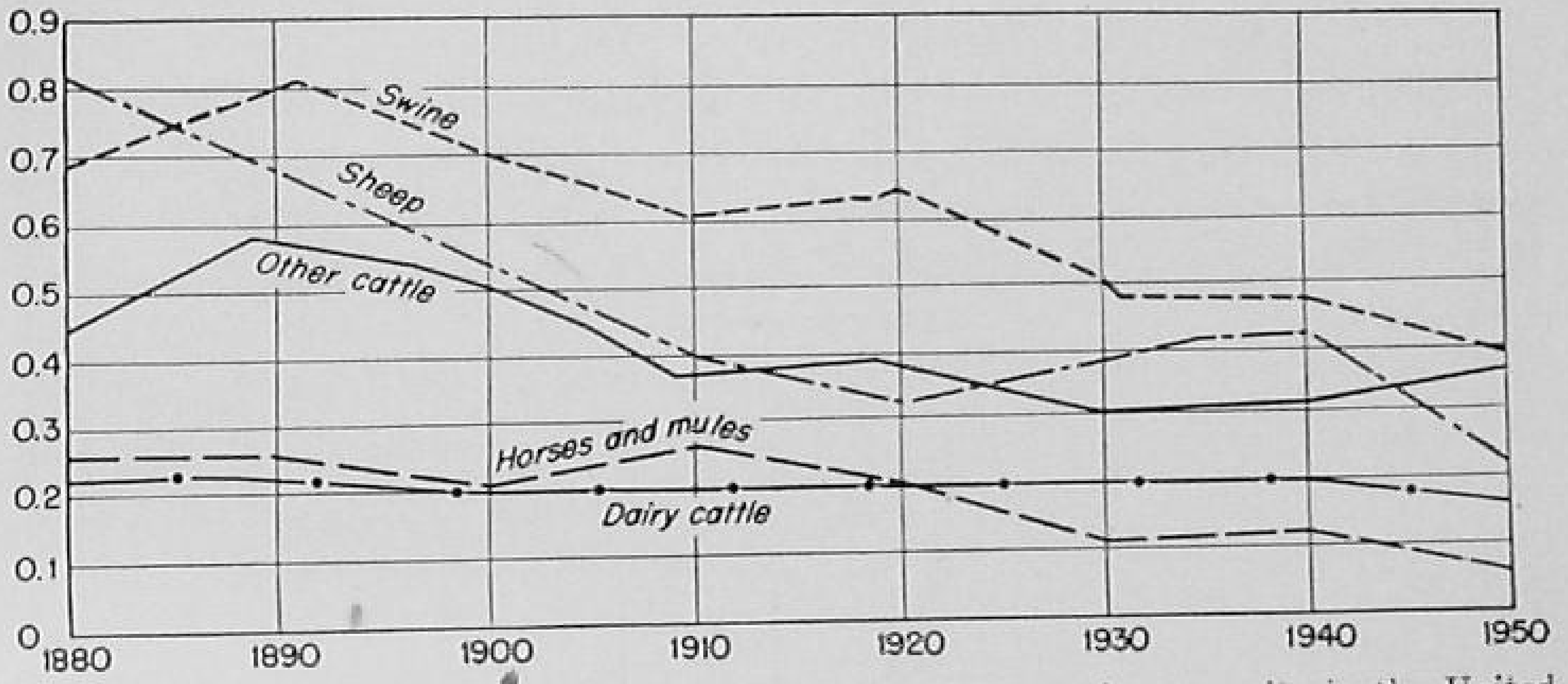

FIG. 1.—Graph showing number of various classes of livestock per capita in the United States, 1880–1950.

of meat would provide about as follows: for 3 meals we could have 7.5 oz. of beef and veal; for 1 meal we could have 1.5 oz. of lamb; and for 3 meals we could have 7.0 oz. of pork, leaving 14 meals each week without any meat. Or the 45 oz. of meat (2 lb. 13 oz.) we consume on the average each week would give us 1 serving of about 8 oz. for some meal on each of 6 days of the week, leaving 1 day for fish or eggs, or maybe fish-eggs.

It would be possible to maintain a much larger population on primary food products (grain, etc.) because of the unavoidable losses in all animal feeding and the fact that no return is received from that portion of the animal's feed which goes for maintenance and which amounts to approximately one-half. The inclusion of animal products in the diet, however, makes it much easier to provide a balanced diet with all the necessary nutritional elements, including minerals and vitamins, plus the additional important fact of making the diet, to most of us at least, much more palatable and enjoyable. Much energy is stored here on earth in a form

not suitable for human consumption, and there is the added consideration of soil productivity, both of which make animal raising indispensable.

The graph (Fig. 1) shows the trends in the number of different animals per capita in the United States during the past 70 years.

Table 6 gives a picture of the trend in meat consumption per capita in the United States since 1900.

The trends indicated by Fig. 1 and Table 6 certainly do not indicate the passing of animal foods from our diet. Meats are palatable and nutritious and will probably be utilized as long as they can be secured and paid for. At the present time, milk would seem to be an indispensable article of diet, and Fig. 1 shows that dairy cattle are maintaining their numbers in relation to population. If they are increasing in average yield of production, there is certainly no less milk being consumed per capita by an increasing population.

Dietary standards, coarse feeds, and climatic and soil conditions would seem an effectual barrier against the passing of livestock. Increasing population means an increased demand for food of all kinds; hence no time should be lost in raising the efficiency of food production to the

TABLE 6.—MEAT CONSUMPTION PER CAPITA, UNITED STATES
In Pounds

Year	Beef	Pork*	Lamb	Veal	All meats
1900	67.0	65.3	6.5	5.2	144.0
1910	70.5	66.9	6.4	7.2	151.0
1920	59.1	63.9	5.4	8.0	136.4
1930	48.9	69.8	6.7	6.4	131.8
1940	55.2	64.4	6.6	7.3	133.5
1948†	63.4	68.3	5.0	9.4	146.1

* Excluding lard.
† Tentative.

highest possible level. In such a program there will surely be found a place for all the really efficient animals that can be produced.

The place of farm animals in converting rough feeds into usable form for the human animal, in improving our American diet, and in conserving and increasing soil fertility has long been realized. But an increasing spirit of awareness of the major role which animals are destined to play now pervades, and livestock production is now often referred to as animal agriculture. We now see that our so-called surpluses of grains can best be stored in animal hides. This at one stroke provides a reserve of food for emergency and a better fed populace and is in full keeping with the idea of an economy of abundance.

The data in Tables 1 and 2 show that the number of dairy cattle, beef cattle, sheep, and swine compared to human population has steadily declined, starting at a high of 2.64 of these animals to each person in the United States in 1880 and decreasing by 10-year intervals through 2.40 in 1890; 2.05 in 1900; 1.67 in 1910; 1.59 in 1920; 1.34 in 1930; 1.33 in 1940; and 1.16 in 1950. Increasing production in dairy cattle, faster maturity, and meatier carcasses in the meat classes have, of course, tended to offset the decrease in numbers.

The Bureau of Agricultural Economics has reduced all food-producing livestock (meat animals, dairy cows, and poultry) to a hog-equivalent basis. They report that in 1920 we fed 1.67 head of producing livestock per capita; in 1930 the figure had fallen to 1.55; in 1940 it stood at 1.53; and in 1948–1949 it was 1.41. There are two possible ways of storing grain—in dead storage or in animal hides. When stored in the latter way, we have an emergency food supply, we have a chance to increase our soil fertility, and we have a better nourished populace consuming more milk, meat, and eggs.

H. E. Babcock estimated in 1948 that for the proper nourishment of 150 million people, we would need an additional 10 million dairy cows, 11 million beef animals, 8 million sheep, 20 million hogs, and 120 million poultry. It is obvious that we need increases both quantitatively and qualitatively in all our classes of livestock. To an extent greater than the average person realizes does the future welfare of the United States hinge and depend upon these gains in animal agriculture.

Present Status and Problems.—Many animals are unprofitably low or inefficient producers because they are poorly fed and cared for. If the average horse were well fed and cared for and were thus able to work and breed at maximum efficiency, if the average cow, ewe, and sow were performing at somewhere near the maximum set by their inheritance, livestock farming would be much more profitable than it now is. This involves also the control or elimination of our various and sundry livestock pests and diseases, which take an annual toll of millions of dollars in terms of lowered individual and breeding efficiency. Likewise, our civilization would be on a much higher plane if each human individual were performing more closely to his inherited capacities. The problem facing us, therefore, as far as our animals are concerned, consists of feeding and managing what we have more efficiently as well as raising the level of capabilities through selective breeding.

In one sense a treatise on the breeding and improvement of farm animals seems rather futile without its corollary, the breeding of better men, for if our human inheritance and environment were better and we could induce our people to live and work more nearly to the upper limit of their

capabilities, there would be less need to write books about breeding better livestock. An encouraging angle, however, is the fact that the principles underlying the creation and maximum productivity of livestock are identical with the principles underlying these things in man himself. If we can put the principles to work generally with our livestock, they will perhaps gradually become incorporated in our thinking about ourselves.

In our animal breeding we must, of course, start from where we now are, with what has come down to us from the past. The genetic task in the field of breeding, therefore, is twofold: (1) to find out what we have genetically, in other words, to analyze; and (2), to raise the average level

FIG. 2.—Jersey Bull, Count St. George. First-prize bull in 1882. (*Courtesy of American Jersey Cattle Club.*)

of production and efficiency all along the line by making better combinations of genetic materials, in other words, to synthesize.

There can be little question about the fact that most of our animals at the present time are mixed in their inheritance. We shall learn later that inheritance is due to the actions and interactions of discrete bodies called *genes*, which are found associated in groups, each group of genes making up a *chromosome*. The chromosomes (*chroma* the Greek word for color, and *soma* the word for body) are found in the nuclei of cells. Each species of plant and animal has a definite, permanent number of chromosomes. If a member of the Shorthorn breed of cattle got the gene, or determiner, for red color (R) in a chromosome from its sire and its allele for white color (r) in a chromosome from its dam, its genetic make-up would be Rr and its color roan (*i.e.*, RR = red, Rr = roan, and rr = white, there being no dominance between genes R and r). Such an

animal cannot breed true because it will pass along to each of its offspring either the chromosome containing the gene *R* or the one containing the gene *r*.

This illustrates the two basic concepts of modern breeding knowledge: (1) the mechanism of inheritance is found in discrete bodies (genes) or, in other words, is particulate; and (2) each offspring gets only one-half of the genetic material which its parent possesses; in other words, the inheritance is halved each time it is passed to an offspring. So an *Rr* (roan) animal cannot breed true because it cannot give an identical gene (in this case, determiner of color) to all its offspring. This animal is not pure for color, speaking genetically, or, in technical terms, is *heterozygous*

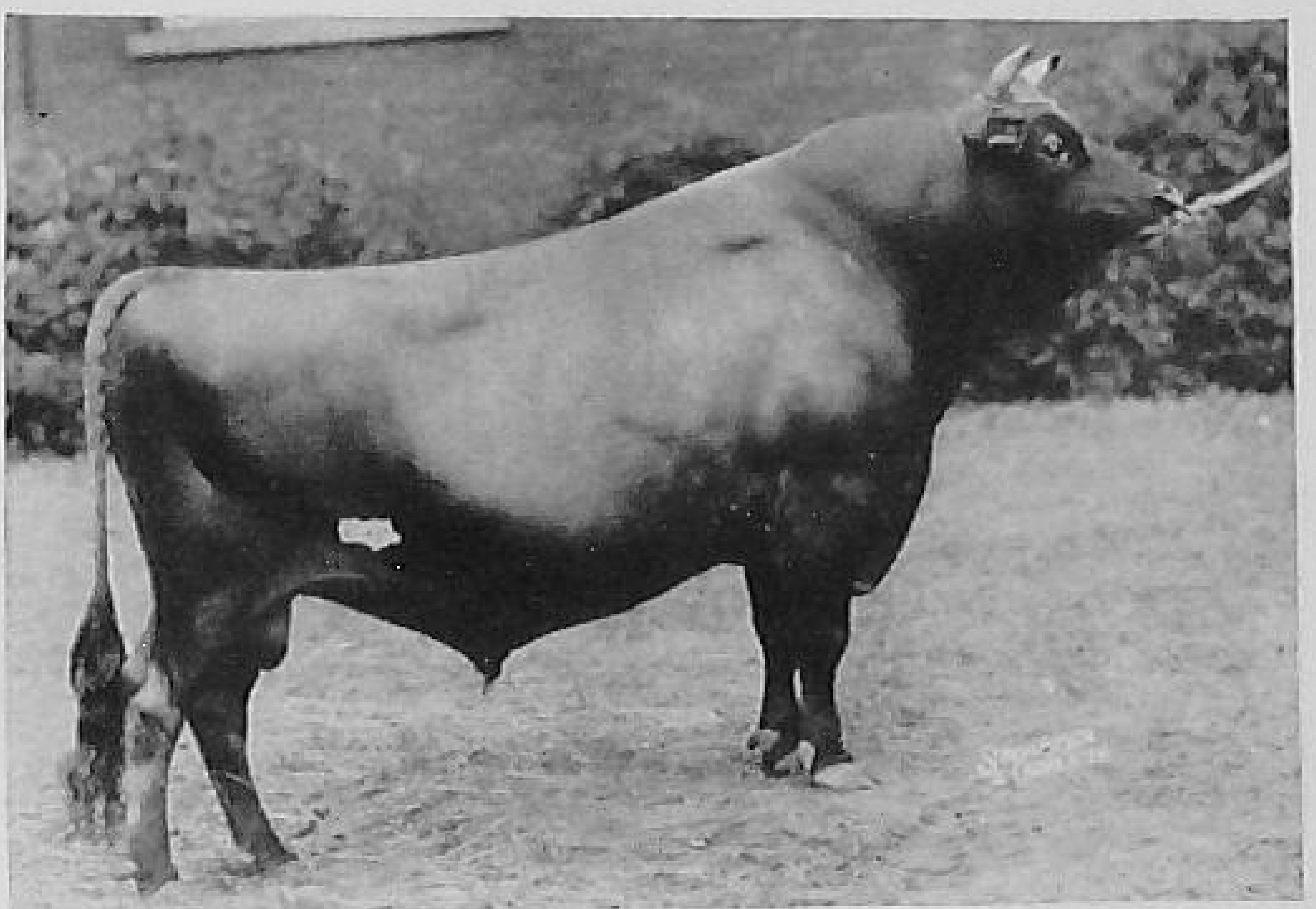

FIG. 3.—Jersey Bull, Brampton Standard Sir, a modern sire noted for the excellent type of his offspring. (*Courtesy of American Jersey Cattle Club.*)

as far as color is concerned. An *RR* (red) or a *rr* (white) animal is pure genetically (for color) or, in technical terms, *homozygous* (for color) and will, therefore, breed true in the sense of passing an identical gene to each of its offspring.

Our breeds of livestock are pure, or relatively so, for certain distinguishing color markings, for horns or for no horns, etc., but they are not pure for the genes that determine commercially valuable characteristics. They have been made pure or homozygous for their superficial trademarks by the process of weeding out those animals which were themselves not pure as evidenced either in their own make-up or in that of their offspring, a relatively simple process in characteristics determined by one or a few pairs of genes acting on distinct and easily recognizable traits.

They are not pure (homozygous) for speed and stamina, rapidity and efficiency of gain and quality of carcass, quality and quantity of meat and wool, amount and quality of milk, etc., simply because we have not

yet ruthlessly culled out those which do not measure up to given standards of production and transmission. We have all sorts of shapes and qualities and productiveness in our livestock, and the animals cannot yet be counted on to transmit as they themselves look or behave. They are heterozygous (mixed) in their genetic make-up and hence cannot breed true or uniformly.

The greatest need in animal breeding today is for records of performance so that we may learn definitely how our animals are transmitting. When we have developed better ways of measuring performance, and physiological studies of different hormone levels have provided new clues

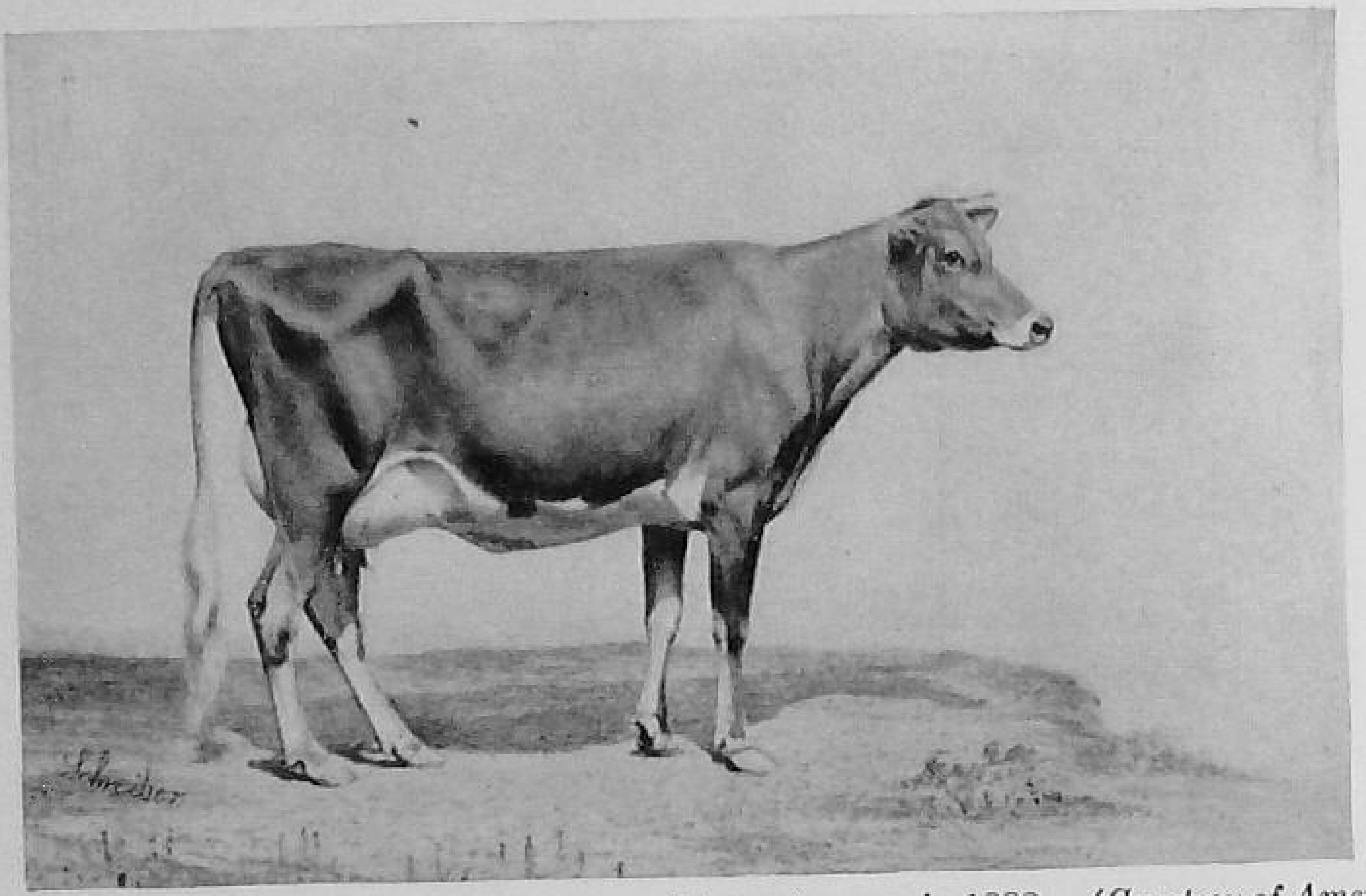

FIG. 4.—Jersey Cow, Khedive's Primrose. First-prize cow in 1882. (*Courtesy of American Jersey Cattle Club.*)

to probable performance, we can intelligently weed out the unfit, breed only from the fit, and so, gradually, purify our stock in terms of their commercially desirable characters.

Breeding Opportunities.—Although it cannot be denied that well-nigh perfect specimens of the various classes and breeds of livestock have been produced and that in practically all breeds the prices paid for individuals have risen well into the thousands of dollars, the fact remains that opportunity is still written large before animal breeders. A few nearly perfect specimens have been produced, and record after record has been established only to be replaced by a better one after a short while.

The record in milk production during 1 year is 41,943 lb. (Carnation Ormsby Madcap Fayne, H.F.), in butterfat 1,614 lb. (Melba 15th of Darbalara, Milking Shorthorn); in speed at the trot for 1 mile, 1 minute

55¼ seconds (Greyhound), at the pace, 1 minute 55 seconds (Billy Direct).

The record in horse pulling contests for heavyweight teams is 4,225 lb. tractive pull, which is equivalent to starting a load of 54,870 lb. on a wagon on granite-block pavement 15 to 20 consecutive times, or more than equal to pulling 10 plows cutting furrows 14 in. wide and 6 in. deep, in ordinary corn-belt black-loam soil. The record for lightweight teams is 3,525 lb. tractive pull, which is equivalent to starting a load of 45,779 lb. on a wagon on granite-block pavement for the same number of times, or more than equal to pulling 8 plows cutting furrows 14 in. wide and 6 in. deep, in ordinary corn-belt black-loam soil.

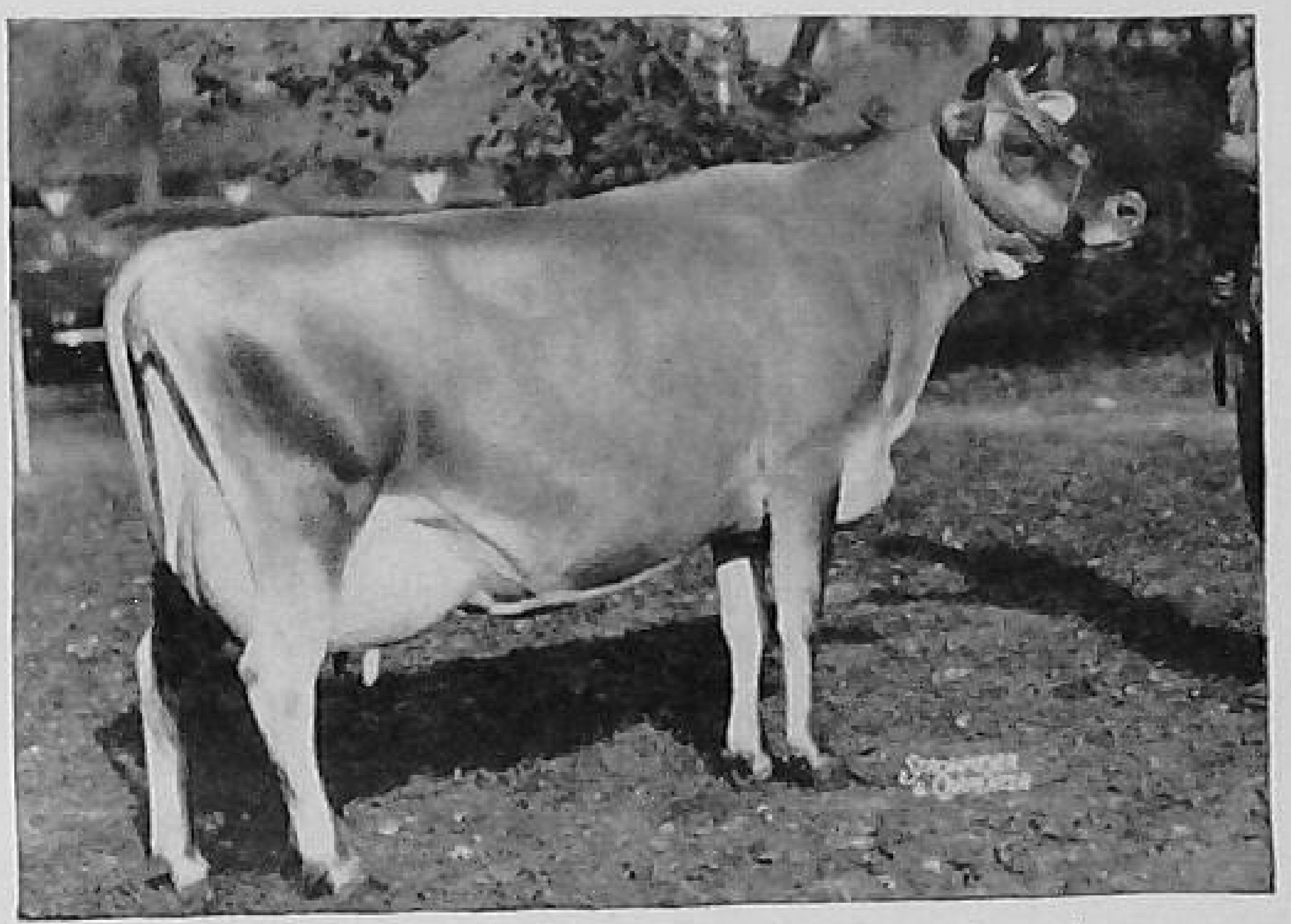

FIG. 5.—Jersey Cow, Sybil Design Etta. Grand Champion Jersey cow, 1947–1948. (*Courtesy of American Jersey Cattle Club.*)

The record in the ton-litter contest stands at 5,117 lb., the combined weight attained by an Illinois litter of 17 pigs in 180 days.

The outstanding Rambouillet sire, Prince of Parowan, owned by the Bureau of Animal Industry, produced seven annual fleeces of wool that averaged 31.5 lb. per fleece, unscoured, an outstanding record of long-time wool production. This wool yielded about 40 per cent of clean wool, or 12.6 lb. of actual wool, per fleece. A large percentage of several hundred of the best Rambouillet sheep in the flocks of the Western Sheep Breeding Laboratory, Dubois, Idaho, are descendants of this ram.

The ability of the goat to produce milk is evidenced by the fact that the highest official test on record in the United States was made by a French Alpine doe, Little Hill Pierrette's Lady Penelope, that produced 4,632.3 lb. of miik in 10 months, an average for the period of 7.2 qt. a day, a figure not far below the average production of all dairy cows in America.

An idea of the opportunity for improvement within a particular breed of beef cattle by breeding and selection may be gained from some of the Bureau of Animal Industry record-of-performance data with steers, which show a range in efficiency all the way from 12.01 to 24.47 lb. of live weight gained for each 100 lb. of total digestible nutrients consumed. The number of days from birth to 900 lb. live weight varied from 412 to 591.

FIG. 6.—William Duthie of Collynie, a Shorthorn breeder who held annual sales for 39 years and sold 1,022 head, mostly bull calves, for a grand total of $1,238,-646. (*Courtesy of Breeder's Gazette.*)

With dual-purpose cattle, the breeder is confronted simultaneously with the two variables—milk production and beef production. The variation in efficiency with which beef is produced by the dual-purpose animal is similar to that in the beef breeds. In the bureau's work with milking Shorthorns, the variation in efficiency covers a range of from 11.49 to 21.38, and the number of days from birth to 900 lb. live weight extend from 358 to 532. Milk production varied from less than 5,000 to as high as 12,000 lb.

All these records, when compared with the average performance of our livestock, indicate the tremendous opportunities still existing in the field of breeding. These top-notch animals resulted from certain combinations of hereditary units plus, of course, excellent care, feeding, training, and general management. As we shall learn later, there are literally billions of ways in which the hereditary chromosomes can be recombined. Our first job is to learn the genetic make-up in our livestock through careful record keeping and then to recombine the units into more desirable combinations through systems of breeding and selection.

Breeding is the improvement of animals through rational selection of germ plasm and full development of resulting somatoplasm. A cursory glance at the qualifications requisite in one who is to improve animals removes at once any surprises at the scarcity of such breeders. Men like Bakewell, Cruickshank, Col. Taylor, Lothrop Ames, Gentry, Duthie, Marsh, and a score of others of greater or lesser fame are, comparatively speaking, very rare because of the size of the task and the multiplicity of details with which a breeder must deal.

Successful breeders are equipped with keen powers of observation, are thorough students of animal form and function who are able to select and mate wisely, are good farmers and intelligent feeders who can bring to full expression the inherent potentialities of their animals, and they are not deficient in business acumen, which makes possible the accumulation and wise use of capital. They are the type of men who inspire loyalty and fairness from those with whom they come in contact. In short, successful breeders are usually hard-working, practical idealists who appreciate the privilege of working with the Creator in molding nature's forms more closely after some ideal by means of records of performance, systems of breeding, and selection.

The Purebred Era.—The rise of the present-day pure breeds of domestic livestock dates back a comparatively short time. Practically all of them arose during the eighteenth and nineteenth centuries. At that time, breeders began to be guided by more definite ideals of type, to have greater recourse to assortative matings (like to like) which soon led to the necessity of various degrees of inbreeding, which tended to fix the characteristics they desired. In terms of genetics, they took a very heterozygous strain, inbred it, which sorted it out into homozygous form, and then disposed of those undesirable animals which no doubt carried double sets of recessive factors. Such methods are still efficacious, but it is a question whether or not they are being used as much as they might well be.

The term "purebred" may in some instances be something of a misnomer. For example, the term "purebred dairy cow" should imply, it would seem, that the animal in question is capable of producing large quantities of milk. It does not, of course, imply anything of the sort but only that the animal's sire and dam were purebred. Our dairy breeds are relatively pure for color, size, etc., but they are not yet pure for high milk production, though, of course, by proper methods of selection they can be made so. It would be much better to speak of these animals as "registered" rather than as "purebred" and to use this latter term only in its genetic sense. The term purebred, however, has gained such a place through common usage, that it would be futile to oppose its use. The student, nevertheless, should be on his guard and cognizant of the various shades of meaning of the term purebred.

The first herd book, for keeping Thoroughbred pedigrees, was a private affair started in England in 1791 to be followed by another private herd book for Shorthorns in 1822. None of our purebred registry associations in the United States is as yet eighty-five years old. Pedigrees for the Thoroughbred horse and the Jersey cow were first kept in America in 1868, for the Corriedale sheep in 1915. There were 11 of the more impor-

tant breed associations formed in the decade 1870–1880; 13 in the next decade, 1880–1890; 6 in the next, 1890–1900; 2 in the next, 1900–1910; and 3 in that from 1910–1920. The average date for the founding of the cattle associations was about the year 1870, for horse and swine associations about 1880, and for the sheep associations about 1890. However, new breeds are still being formed and new breed associations established.

Men with common interests in the same breed of livestock banded themselves together into breed associations for two prime reasons. One of these was to protect the purity of the breed in order that it might retain its distinctive external trade-marks or to keep out the genes that determined characters not wanted. This was to be accomplished by a system of registration open at first to animals that met these certain trade-mark qualifications. This practice in due time was to be superseded by the stipulation that only the offspring of registered animals were to be eligible for registration. Because no stipulations regarding ability to fatten or to milk, etc., were or ever have been set up, it is not to be wondered at that poor producers were originally admitted into the select circle of the purebreds and that there are still some to be found there. For many years any horse could be admitted to the Standardbred Register for horses on successfully meeting certain requirements for speed. The only criterion for the admittance to registration of a calf of the dairy breeds is that its sire and dam be registered animals of the same breed and the calf show no disqualifying characteristics. In the one case the criterion was performance with no questions asked about parentage. In the other it is parentage with no questions asked about performance. Perhaps the first system was wrong, certainly the second is, and the best system would include stipulations regarding both performance and pedigree.

Some of the breed associations, having realized that much poor germ plasm is to be found in all breeds, are now struggling to devise means of selective registration. Rules that will be genetically sound and commercially fair as well as practicable for this sort of thing are very difficult to formulate. If the difficulties prove insurmountable, an alternative method would be something similar to the herd test in the dairy breeds. In this system every female in the herd must be tested, *i.e.*, her milk weighed and its butterfat percentage determined, and the poor producers thus can be eliminated from the herd average by surrendering their registration papers. If this practice could be made widespread and all the facts published, the breed would gradually purge itself of its poor germ plasm, assuming that no dairyman would use a son of a bull which had demonstrated his own lack of the genes for high production through the low production of his daughters. Such a system is very slow, perhaps too

slow, and a bull may have many daughters as well as many sons in service before his own poor inheritance has had time to show itself in the first 5 to 10 daughters' production. Low official-type classification also requires the surrendering of registration certificates or the prevention of further registrations.

The other prime function of the breed associations was that of promoting its particular breed. This led to some very worth-while competition between the breeds and some, perhaps, that was not very much worth while. Much of this early breed-promotion work was based on superficialities, largely perhaps because the real basis for animal improvement was at the time unknown. Excessive fat was utilized to produce even contours, cows were forced to abnormally high and probably uneconomical milk production in order to "sell" the breed. Breeds were judged, by the unthinking, in terms of a few superlative accomplishments rather than in terms of their average level of merit. Demand for purebred sires was very brisk with the result that every breed retained much poor germ plasm, and a lot of it is there to this day. To get a purebred sire seemed to be the easy and quick way out of all our breeding difficulties. This attitude is found in all fields of human endeavor. We want to get to our goal by a quick and easy method, so we take various and sundry short cuts, but, unfortunately, they seldom or never lead us to our goal. Breeding better livestock is a slow, tedious process. If we use proper methods, we can hope to make some progress, but we should beware of short cuts and panaceas.

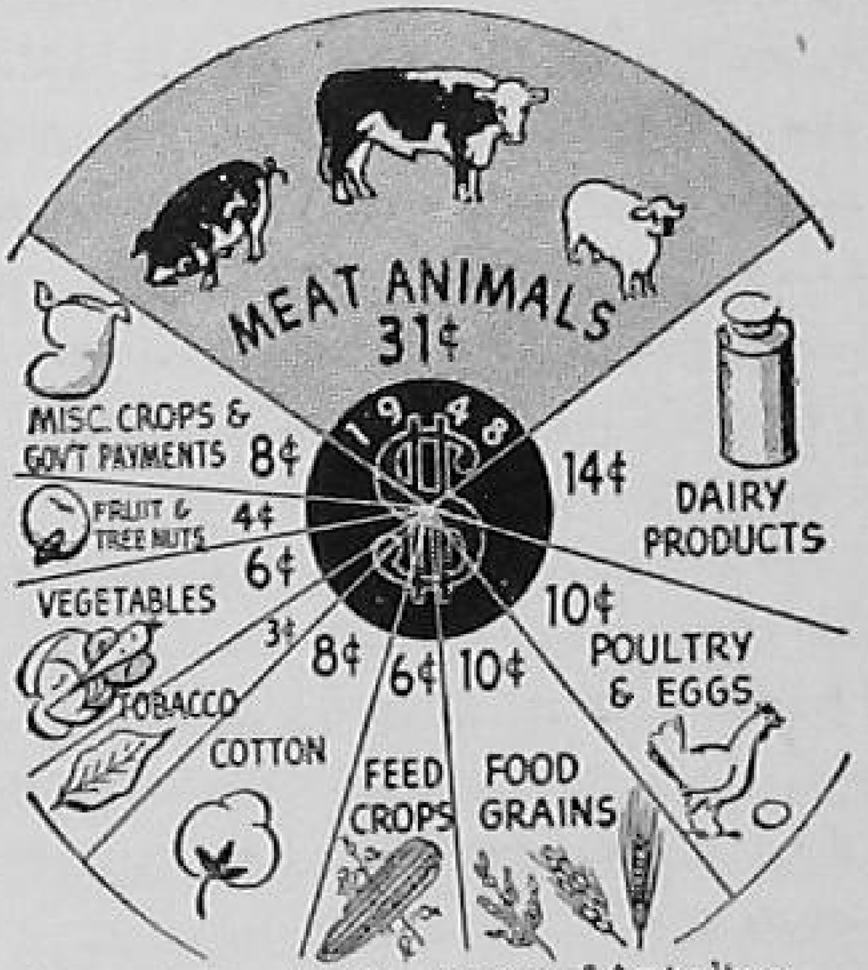

FIG. 7.—Sources of the American farm dollar in 1948. (*Courtesy of U.S. Department of Agriculture.*)

The breed associations also set the ideals for their breeders largely through the awards made at livestock shows. The breed associations have always exercised their right to have something to say about who shall judge at livestock shows. Many of them publish lists of acceptable judges, and some of them conduct judging schools to train judges in breed ideals and to encourage uniformity in placings in different sections of the country. In brief, they try to mold their breeds after acceptable standards of perfection. In all this up to the present, there has been no compulsion. Each breeder is free to follow his own bent, to test or to show

or not to do so. Any breeder is free to attempt to change the presently accepted breed type, and the types have been changed many times, presumably in accordance with changing market demands.

Our purebred breed associations have made invaluable contributions to better livestock. That they should not have made mistakes would have been miraculous. Their good far outweighs the bad up to the present, but they still have much hard work to do. Their final task will consist of providing the mechanism for proving the producing and transmitting merit of the animals in their respective breeds.

The title of this section, "The Purebred Era," should not be construed as meaning that the writer believes the purebred has had its day and will pass on. The work of the purebred breed associations over the past 85 years has laid a firm foundation on which a great superstructure of really beautiful and efficient animal types can and will be built. It has been our purpose to pay our respects to the untiring work that the men making up these associations have done and also to point out the ultimate fallacy of protecting breed purity and promoting the use of purebreds without taking the necessary steps to purge the breeds of their undesirable germ plasm by feasible systems for proving breeding merit.

That genetic variations in efficiency in converting feed into milk, butterfat, meat, wool, or power exist among our animals is now well-established through carefully controlled experimental work. Probably there are also genetic differences in disease resistance, maternal characteristics, quality of product, fertility, ease of milking, etc. The next task of the breeder and breed associations is to devise the recording machinery so that these inherited differences may be ascertained and the facts made available to all.

Rise of the Breeds.—For 200 years after the beginning of the settlement of North America, the early settlers and later immigrants brought livestock to these shores, as none of the larger farm animals were here when they came. These were the native stock of their respective native lands. There were no breeds as we use the term today, although local varieties of animals have probably been continuously developed in all parts of the world for the past few thousand years. Certainly that was the case in early America, and some of these creations have persisted and developed into well-established breeds.

The early settlers needed transportation, especially when the country began to expand westward, and naturally turned to the horse. Through selection, there was gradually developed a sturdy, sure-footed, intelligent, and easy-riding horse that was later to provide one of the foundation stones for the American Saddle Horse, the latter breed also having infusions of Thoroughbred, Morgan, and Trotting blood. The need for

a means of travel was met in a practical, matter-of-fact way, and to these basic fundamental traits were added later the refinements of form and style to make some of man's finest creations, the American Saddle Horse, the Tennessee Walking Horse, the Quarter Horse. The story can be repeated for the American Trotter and Pacer, for the Chester White, Duroc, Poland-China, and Hampshire breeds of swine, and for a few breeds of sheep, and for one breed of cattle.

We have seen that the mean date for the founding of our livestock breed associations in America was about the year 1880. This was preceded by a period of about 50 years of final preparation. The average mean date for the introduction from other parts of the world of the local varieties of horses that later became recognized as distinct breeds was about 1820, for cattle 1830, and for sheep and swine 1840. During the years from 1830 to 1880, when the breed associations were formed, strains of red, black, white, belted, or spotted hogs were developed; likewise strains of trotting, saddle, general-purpose, and draft horses; of black, red, black and white, red and white, light or dark-fawn cattle; and of sheep of varying sizes and qualities of meat and wool. Through a gradual process of selection, involving both external trade-marks and intrinsic abilities to render some sort of service to man, the stage was set for the formation of breed associations, each group of men with somewhat similar likes and ideals banding together so as to be able to trace pedigrees more accurately and to merge their efforts of promotion.

All our breeds, foreign or American formed, are of relatively recent origin. All of them arose by the same process of choosing certain combinations of characters from the general inheritance that makes up cattle or horses, swine, sheep, goats, dogs, etc. Our breeds arose from a grand and glorious mixture, and as yet we have purified them only for their less intrinsically valuable qualities.

The exact origin of a breed, old or new, can never be accurately known. This point needs no elaboration for the old breeds. But suppose that we set out to create a new breed by crossing Guernseys and Holsteins. In the first-cross animals we would know that one-half of their genetic material had come from one breed, one-half from the other; but when we mate two of these crossbreds, we have no way of telling what each one is transmitting. Assuming there are 60 chromosomes in cattle, then the hybrid has 30 each from the Guernsey and Holstein breeds, or 60 in all. Each individual, however, transmits only half of its own genetic material to each of its offspring, so that in one case the first-cross animal might transmit 15 chromosomes from each of its two original sources. It might transmit 16–14 or 17–13 or 18–12 or any combination up to 30–0, but there would be absolutely no way by which to determine what the com-

bination was. So the exact origin in terms of genetic material for a breed either old or new can never be known.

Before the advent of breeds, it is logical to suppose that the main criterion for selection was utility. The halo attached to or developed around the term *purebred* was responsible perhaps for relegating proved merit to something less than the main criterion in selection. If this has occurred, it is a distinct loss and an impediment that should be dispensed with as quickly as possible. The breeders themselves are the ones who should take the lead in accomplishing this result.

Beginnings of Breeds in England.—During the eighteenth century, agricultural progress in England quickened. By 1700 from one-third to

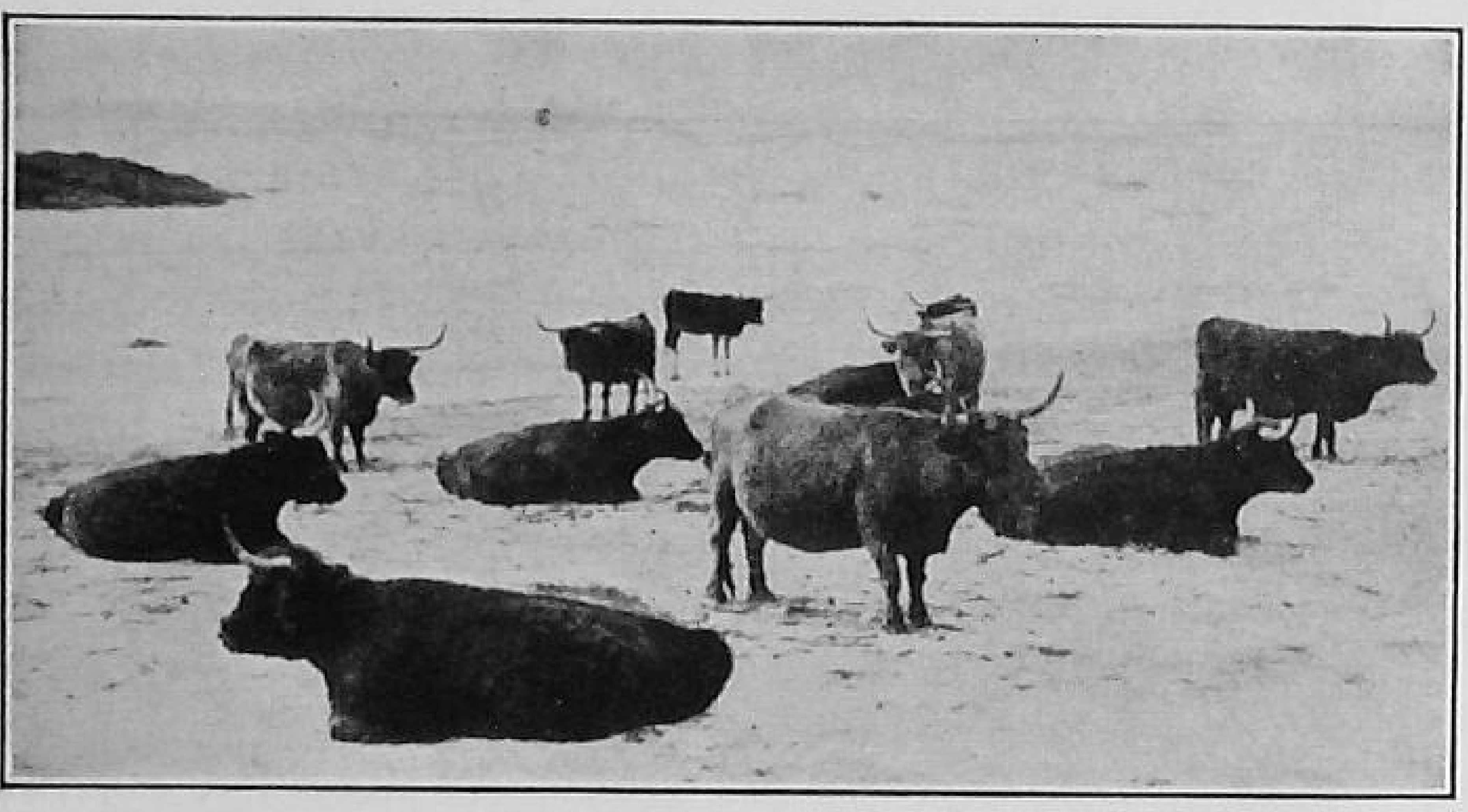

Fig. 8.—West Highland cows, of great antiquity and indigenous to Great Britain. (*From Thompson, Outline of Science, Geo. Newnes, Ltd.*)

one-half of the arable land was still cultivated on the open-field system with its heavy hand laid against more progressive and efficient methods. "No individual owner could attempt to improve his flock or his herd, when all the cattle and sheep of the village grazed together on the same commons." Common lands with movable landmarks and unfenced land with crops often despoiled by passing cattle and sheep led to continuous quarreling and litigation. This type of farming was especially hard on livestock, as the commons were generally overstocked. Writers spoke of "half-starved, greyhound-like sheep," of "animals bearing a closer resemblance to living skeletons than anything else," and of a motley mixture of all the different breeds of cattle and sheep at present known in the island, many of which are diseased, deformed, small, and in every respect unworthy of being bred from. It was claimed that 5 acres of individually owned pasture would have been worth more than pasture rights over 250 acres of common. Enclosing started about 1450 and

progressed at different rates in different parts of England, sometimes by agreement, sometimes by acts of Parliament.

With the change from open field to enclosure, better methods of farming became possible. The great pioneer and the "greatest individual improver" that English agriculture had ever known was Jethro Tull, who published a book, "Horse-hoeing Husbandry," in 1733. He developed a drill for planting seed in rows and practiced clean cultivation to destroy weeds and conserve moisture. The rank and file scoffed at his ideas, some of which became established in Scotland before they did in England; but large landowners gradually adopted his suggestions, so that they eventually spread over England revolutionizing the whole field of agricultural practice.

With the coming of field cultivation of clover and artificial grasses, sometime after 1600, and of roots somewhat later, a great impetus was given to agriculture and livestock breeding. Winter feed could now be had, more livestock kept, more manure produced, better crops grown, still more livestock kept, etc., over and over. This provided both the necessity and the possibility for improving livestock. There had grown up a great variety of short-wool sheep in many sections of England. There were also a number of long-wool breeds, and in general their type was more uniform than that found among the short-wool sheep. Some attempts were made in the latter part of the seventeenth century to improve the breeds, but they were generally made in terms of fancy points rather than practical ones.

In cattle, size alone seemed to rule in selection rather than quality of carcass or earliness of maturity, though power at the yoke and milking quality were early criteria for selection. Here again each county had its varieties, more or less true to some color, length and set of horns, etc. Among these breeds were the Shorthorn, Middlehorn, Longhorn, Devon, Hereford, Sussex, Pembroke and Red Glamorgan, West Highlands, Ayrshire, Galloway, and Angus. Perhaps the quest for size reached its zenith in the Lincolnshire Ox, standing 19 hands high and measuring 4 yd. from his face to his rump. "Stock breeding as applied to both cattle and sheep, was the haphazard union of nobody's son with everybody's daughter." Prizes were offered for the animal with the longest legs, necessary enough perhaps at the time.

Robert Bakewell of Dishley (1725–1795) had the imagination to picture the future needs of a growing population in terms of meat and set about creating a low-set, blocky, quick-maturing type of both sheep and beef. He also worked with the heavy Blackhorse, shortened his back, brought him closer to the ground, replacing height and weight with activity and strength. Bakewell paid little or no attention to fancy

points but bred for animals that would weigh heavily in the best joints and show efficient feed conversion and quick maturity.

His success was due largely to three factors. (1), He had a definite aim in mind and bred for it consistently. Joints preserved in pickle hung from his walls, and skeletons of his most famous animals adorned his halls. (2), Bakewell divorced himself from the common practice of crossing breeds, which tends to dissipate good qualities, and adopted in its place the practice of "breeding the best to the best" regardless of relationships. This meant a considerable amount of inbreeding, a practice generally taboo in the England of that day. Finally, he let for fancy prices, rather than sold, his males; in other words, he got his neighbors to "prove" the transmitting abilities of his sires for him.

It was with the old Leicestershire sheep that Bakewell's success was outstanding. From large heavy-boned and -framed animals with little or no propensity to fatten quickly, Bakewell gradually brought them closer to earth, gave them blockiness of form, fineness of bone, and quick-fattening propensities, which set them off from their forebears as a new variety. Other breeders with animals better fitted to their respective localities were soon following Bakewell's example with the Leicestershire, and it was not long before Leicesters were closely rivaled if not surpassed.

Working with Lancashires, or Craven Longhorns, Bakewell evidently went too far in establishing better beef qualities at the almost total expense of milk. Since the region, Leicestershire, was also a dairy region, this was fatal, and the Durham Shorthorns bred by the Collings along the lines laid down by Bakewell largely supplanted the Lancashires. Breeders of other breeds soon followed the trail blazed by Robert Bakewell. Animal breeding of this sort became fashionable and respectable and enlisted the services of many country gentlemen.

How great was the change can be seen in the weights of animals at the famous Smithfield Market. In 1710, beeves had averaged 370 lb.; calves, 50 lb.; sheep, 28 lb.; lambs, 18 lb.; whereas in 1795 they were 800, 148, 80, and 50 lb., respectively. Individual initiative encouraged by enclosures, the introduction and use of turnips and clover, the labors of agriculturalists like Tull and Townshend helped enormously to bring about these changes. But the main influence was that of Robert Bakewell, whose imagination, initiative, and courage put a firm foundation under improved methods of livestock breeding. Animals and man had progressed slowly together for 10,000 or 20,000 years. Latent in both was the promise of a better tomorrow. To Bakewell above all other men belongs the credit for loosening the shackles that held animals back. Using the crude principle of "like begetting like," he molded animal

inheritance into a preconceived pattern through close breeding and selection. This system, then as now, leads to purity or homozygosity. When other breeders adopted Bakewell's methods, the foundations of our modern purebreds were laid.

Late Middle-Ages Agriculture of England.—During the Middle Ages (500–1500) in England, as elsewhere, rotation and improvement of crops and improved breeding methods were not a necessity because virgin soil was abundant and worn-out lands could be deserted for new. Increasing population and the establishment of settlements were later to make improved husbandry a dire necessity. Thus wild field-grass husbandry was supplanted by the permanent separation of arable land from pasture-land. The former was the system in vogue during feudal days in England from the eleventh to the fifteenth centuries. At this time there were four types of land: (1) the demesne or lord's land, (2) the free land of the military service or rent-paying men, (3) the unfree land worked by various classes of bondsmen, and (4) the common pastures and untilled wastes. Each manor was self-sustaining, and there was but little trade in agricultural products. "For such ready money as he needed, the lord looked mainly to the produce of his livestock."

Horse farms appear in the accounts of some of the manors in the thirteenth century, probably supplying the "great horse" for military purposes. Cart and plow horses were to be found on most farms and were often worked along with oxen. The latter were steadier, easier on the harness and plow gear. The winter keep of oxen was less than that of horses. They needed less care, were less liable to sickness, and on death yielded both a hide and a carcass. Attendants of both classes slept in the barns with their charges.

Cattle fared badly in these early days. Pastures, never very plentiful, were generally overgrazed so that fresh-butchered meat was seldom eaten. Aged animals and worn-out oxen were prepared after a fashion through the summer for slaughter in the fall and then eaten fresh, or salted for winter use. Winter feed was scarce with the result that spring generally found the cattle in a very thin weakened condition.

Dairy cattle fared little better and produced four-fifths of their yield during the 24 weeks of summer. In the winter milk was worth three times its summer price. Calves were poorly grown because of the human demand for milk. Much use was made of all sorts of cheeses and much summer butter was preserved for winter use.

To the medieval agriculturalist, sheep were the sheet anchor of farming. Their chief product was not meat, milk, or hides, but wool. From earliest times, districts like Shropshire, Leominster, and the Cotswolds had been famous for their wool. The high prices paid for rams is evi-

dence of an attempt at better breeding, though the presence of scab and rot made sheep raising a risky venture. The shepherd's task was one of the most important ones on the farm, he was respected above most others, and lame shepherds were in great demand because a lame man was not likely to overdrive his sheep.

Pigs were held in high favor and valued as more profitable than a cow. They were also invaluable as scavengers. Turned loose, they were self-supporting during all except 3 months of the year. At farrowing and fattening time they received some extra care and feed. In type they were rangy, lop-eared, and agile. What selection was practiced was based largely on the animal's ability to fend for itself, "root hog or die."

To sum up the status of livestock in thirteenth-century England, we have seen that types of animals to fit the contemporary need had been developed, but that means of adequate feeding or very high ideals of better breeding were sadly lacking. Nevertheless an adage of the time ran, "He that hath sheep, swine, and bees, sleep he, wake he, he may thrive."

The open-field system, including the arable land, the meadow, and the permanent pastureland, prevailed quite generally in England at some time or other, and examples could still be found up to the eighteenth century. The manor system of farming tended to break up between 1300 and 1485, largely because the lords became more interested in sport and war than in improving farming practices. Famine followed, owing to lack of interest by the large owners and the lack of resources of lesser men. Whatever improvements were registered were largely the contribution of monks, winter was a season to be dreaded. Gradually, and for a variety of reasons, the manor system with its graduated mutual dependence began to break up and was supplemented by a system that involved greater individual independence.

The Black Death (1348–1349) hastened the breakup of the manors as it increased the lord's land but greatly decreased the available labor supply. Rents fell, wages rose, and extensive legislation designed to aid the landlord could not stem the tide of manorial breakup. More and more small separate farms came into being that were let out for money rents to individual occupiers. Freeholders, leaseholders, renters, and free laborers increased at the expense of the class of villeins.

Thus, shortly before 1500, feudalism in England practically ceased to exist—the Middle Ages were supplanted by modern times. Feudalism was followed by enclosure. Open fields and pasture commons were enclosed, sounding the death knell to the old medieval agrarian partnerships and signifying the birth of individual ownership. The rise of a very profitable wool trade as well as the increased demand for meat turned

much arable land into pasture, much of the change being unwarranted. Land now came to be thought of in terms of what rent it could earn; in other words, agriculture became commercial.

Grass holdings were enlarged at the expense of tillage in order to accomodate the sheep-farming craze. In the process many small farmers were ruined and many once happy villages became "deserted." Laws passed to preserve farm homes and buildings and to require tillage were easily circumvented, and preachers and versifiers inveighed against sheep farmers and the sheep themselves. But the greater efficiency of enclosed land, owned and worked by an individual, over open land, jointly owned, gradually made itself felt, and a new era of progressive agricultural development opened for England. The price for enclosing some ¾ million acres was the throwing out of work of around 35,000 persons. That there was much suffering can be assumed from the numerous rural uprisings of the time, but there were also attempts to deal fairly and adjudicate liberally.

Unaccompanied by a contemporaneous development of arable land, enclosures caused a growing scarcity of employment. Tenant farmers, copyholders, squatters, cottagers, and laborers suffered alike, and the rise in the cost of living pushed many to the brink of starvation. Some individuals waxed rich through enclosure, so that the growing unequal distribution of wealth brought many abortive attempts at legislative relief for the unfortunate. Petty crimes, kidnapping, livestock stealing, and similar misdemeanors grew in the rural districts, though a goodly part of it was doubtless perpetrated by disbanded soldiers, adventurers, and other ne'er-do-wells.

During the reign of Elizabeth (1558–1603) "wool was the chief source of the wealth of traders and of the revenues of the crown" and controlled the foreign policy of England. Short wool had serious competition from the Spanish Merino. Ryeland was the preeminent short-wool breed, its center at Leominster and "Lemster ore" the equivalent of "golden Fleece." The Cotswolds led the long-wool breeds with Lincolnshires close behind.

On the whole, there was not much change in the sixteenth- as compared with the thirteenth-century agriculture in England. Some gains were registered, *e.g.*, the greater use of iron in the implements used, but artificial grasses and roots were still unknown, hops the only new crop. Seasonable operations remained about the same, with magic and superstition still controlling plantings and breeding operations. Sheep were considered the "most profitable cattle a man can have," though without turnips their full value could not be realized. Ewes were still milked, and the writers of the time have "nothing to say about the improvement

of breeds of cattle for the purposes that they serve." The general-utility animal was still the ideal. The combining of crop production with livestock feeding was yet to come.

Medieval Continental Agriculture.—In Western Europe conditions were chaotic following the breakup of the Roman Empire, which started in the third century and was complete by the seventh.

The work of reconstruction in Western Europe began in the eighth century. Various rulers, and particularly the Christian church, provided the main impetus. Methods and tools were crude and results in terms of effort meager, but progress was made and the hope of economic security was again revived. Thousands of monasteries were established all over Western Europe, and each of them provided a nucleus for agricultural and livestock-breeding endeavors. Large herds of cattle, horses, sheep, and swine were again established, horticulture and winegrowing again came into prominence.

Even after their adoption of the rudiments of civilized living, the majority of the Celts, Anglo-Saxons, and Germans were largely herdsmen, and in central Germany cattle were still a means of exchange up to the eighth century. The ratio of small animals like hogs, sheep, and goats to larger ones like cattle and horses ranged from 5 up to 9:1.

The period from 900 to 1200 saw the rise and the establishment of feudalism in Western Europe. Land at that time was practically the only capital and it came to be controlled by the ecclesiastical and military classes. Communal ownership of land had changed first to small individual holdings. These were gathered together into great blocks by powerful organizations or individuals. As the saying had it at that time, "no lord without land, no land without a lord." There were still some free men scattered about, but one-third to one-half of all the land, for instance, was owned by the Church and another large percentage by powerful knights and barons. This land was given out as fiefs to be worked by slaves, serfs, half-free, and free peasants. Stated returns went to the lord, and generally the workers also owed the lord or the monastery a stated number of days of work per week.

Nothing, of course, was known of scientific agriculture, and the lot of the peasant and his animals was not a happy one, a horse being worth 100 sous and a peasant 38 sous in the eleventh century. Fallowing was used in place of crop rotation and the cultivation of roots and grasses. Gradually centralized feudal states emerged, nationalism developed, and the monarchies began to revive. This led to extensive colonization all over Europe from the eleventh to the fourteenth centuries. With this came some attention to agriculture, irrigation, development of grasslands

and fodder crops, and attempts to foster an empirical veterinary art and to improve livestock. Studs were set up to try to improve the horse for both war and commerce, and some sections became noted as mule-breeding districts. Cattle also received more attention from the standpoint of meat and milk as well as draft. Small animals, however, continued to dominate, sheep taking the first rank. Millions of sheep were to be found in the Low Countries, France, and Germany, as well as huge migratory flocks in Spain and Italy. There was improved cattle breeding in Scandinavia by the twelfth century, and this region was exporting butter, cheese, fats, lard, and hides. The art of fattening cattle on roots and legumes was first developed in the Low Countries.

The eastern portion of the Roman Empire (the Byzantine) fared better following the crisis of the fifth or sixth centuries. For 1,000 years, it held off or quickly recovered from the onslaughts of the barbarians. It was realized that the two pillars of resistance were agriculture and military art. Through an intelligent system of agricultural colonization, hundreds of thousands of outsiders, including barbarians, were absorbed into this Eastern Empire. Agriculture, animal husbandry, and horticulture flourished, early Greek and Roman agricultural practices were revived, thereby creating the wealth that made this part of the world the envy of all men during the Middle Ages. In the early part of the period the land was held largely by individual owners, but by the tenth or eleventh century most of the lands had gotten into the hands of the Church or of large landholders. Slavery, however, was abolished, and the serfs were accorded privileges and rights, which stabilized rural life with the result that disciplined labor gave to the Eastern Empire its chief economic supremacy.[1]

> The East Roman Empire thus accomplished, during the early Middle Ages, a task of supreme importance. It had received undiminished the heritage of Rome and added to it. It left a profound mark upon every kind of work. It succeeded in colonizing the Christian lands of Eastern Europe and it civilized the barbarians, calling them to the fruitful labours of peace. It gave a powerful impulse to every form of economic activity, and carried the production of wealth to the highest point. If in the social order it only half succeeded in protecting free labour and free property against the exploitation and usurpations of the aristocratic classes, it yet suppressed slavery, and strove with all its strength to maintain the middle class, both urban and rural. Thus it placed itself in the van of civilization, whose great traditions it carried on, and it was partly to Byzantium

[1] Boissonnade, P., "Life and Work in Medieval Europe," pp. 60–61, Alfred A. Knopf, Inc., New York, 1927.

that the West in its turn went to school to be prepared for its own civilizing mission.

Roman Agriculture and Animal Husbandry.—The seven separate hills of Rome, settled at first by humble herders and hunters, were eventually drawn together into the Septimontium (League of the Seven Hills) and destined to become the ruling center of the greatest empire the world had ever known. Agriculture in the surrounding region kept pace with the growth of the city and came to enjoy a real prosperity. The unpaid militia, consisting to a large extent of small farmers, was often called upon to protect the region from invaders, but the campaigns were seldom of long enough duration seriously to affect agricultural practice. This is not true, however, of the period from the First Punic War (against Carthage) in 264 B.C. down to the time of the death of Augustus, A.D. 14.

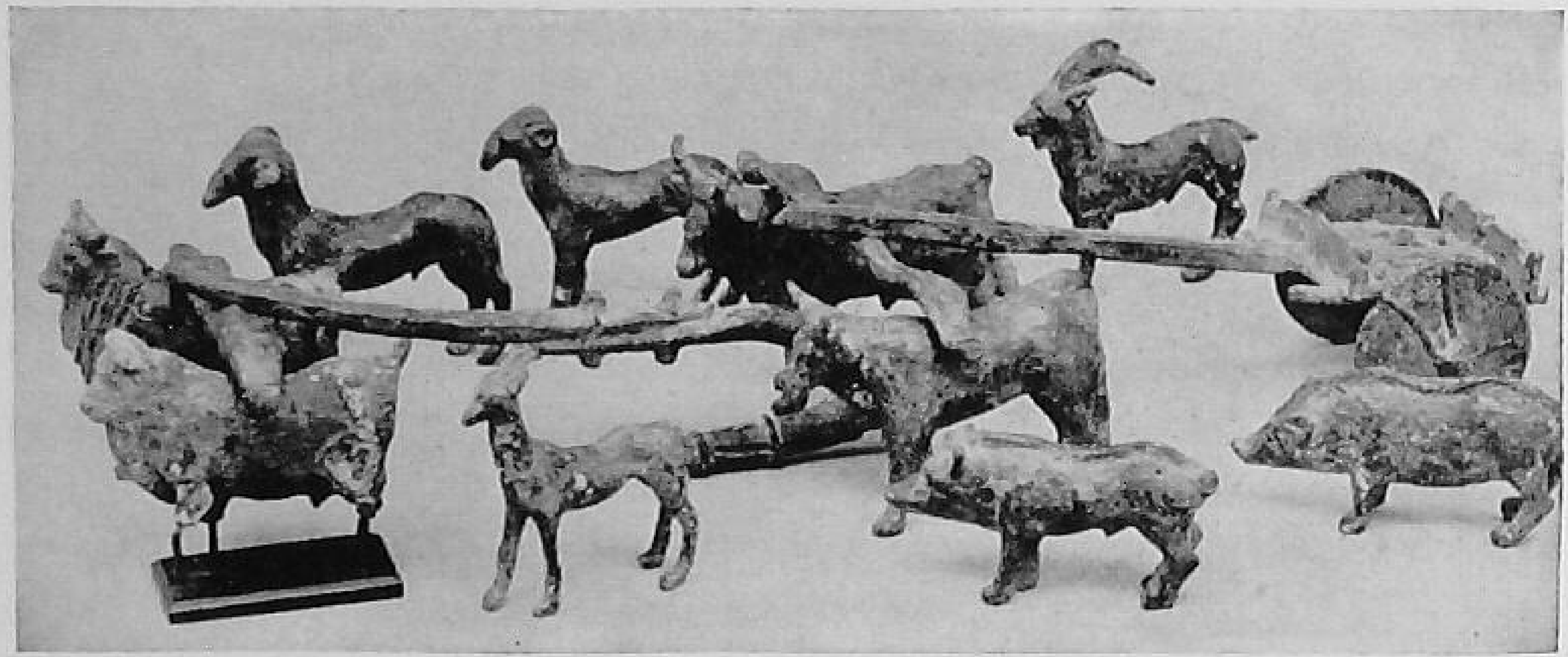

FIG. 9.—Statuettes of Roman animals in bronze, first century B.C. to third century A.D. (*Courtesy of The Metropolitan Museum of Art.*)

These were the times of Roman wars of expansion, and they were long and bloody. The middle-class farmer bore the brunt, was slaughtered by thousands, with the result that a great deal of the property fell into the hands of a few rich owners. In addition, thousands of the conquered were brought to Rome and sold as slaves to work the land. The earlier type of Roman agriculture gradually found itself unable to compete with outlying conquered territories in the matter of supplying grain. The type of agriculture, therefore, shifted to greater numbers of livestock, especially horses, sheep, and hogs, and to increases in orchards, vineyards, and gardens. The country became almost deserted except for foreign slaves and barbarians, the drainage works fell into ruin, and the old unhealthfulness returned.[1]

[1] TOUTAIN, J., "The Economic Life of the Ancient World," p. 234, Alfred A. Knopf, Inc., New York, 1930.

This transformation of rural economy led in the end to a social phenomenon of great importance in the history of Rome. The countryside was deserted by most of the small landowners and free tenants, who came crowding into the towns, and especially to Rome. This influx of poor people, ruined by the new condition of farming, enormously increased the mass of the Plebeians, which was at the same time swelled by increasing throngs of freedmen of foreign origin, Greek and Oriental. There was no longer a balance in the citizen body between the rural elements, which had once been hard-working, productive, and level-headed, and the urban proletariat, which grew more and more accustomed to call upon the State, the magistrates, candidates for office and ambitious men of every kind for its food and amusement—*panem et circenses.* Rome ceased to be the capital of an essentially agricultural people, whose wealth was mainly based on landed property and agricultural resources; it became a turbulent agglomeration, in which industry, trade, and money-dealing assumed an importance hitherto unknown.

The formation of the Roman Empire near the beginning of the Christian Era brought Gaul, Spain, Africa, Greece, and Egypt under Roman influence. Rome demanded economic, political, and religious loyalty but allowed old native traditions, habits, and sentiments to persist, provided they did not interfere with the loyalties she demanded. Economic life in these conquered areas went on much as before, though quickened by inclusion in a greater united whole. Roman legions and fortifications held back the barbarian hordes on all sides and gave a comparatively long period of relative peace throughout the Empire and in Rome itself, when the civil wars were extinguished.

So far as we can learn, there were no great agricultural innovations or livestock improvements either in Italy proper or in the other parts of the Empire during this time. Of a slow, steady evolutionary process, however, we have reason to be assured. Selection, no doubt, went on in livestock breeding, and the long period of peace during the first two centuries of the Christian Era was bound to have had its effects. We get some indication of the relative importance of various types of agriculture in the Empire from the fact that Columella's 13 books *De re rustica* include no whole book devoted to grain growing, 2½ books devoted to winegrowing, about 1 each to fruit trees, including the olive, and to gardens, while livestock occupies 4 books.

The Empire consisted of cities with surrounding agricultural lands, orchards, and vineyards. Beyond were to be found the pastoral nomads with their flocks and herds; and in the hinterland, the barbarians. Each region of the Empire adapted its crops and animals to its particular topographical and climatic conditions. Variety there was to be sure, in lands, in peoples, in methods. Although there were large estates in all parts

of the Empire worked by slaves or tenants, the real backbone of the fabulous old Roman Empire was undoubtedly to be found in the sturdy, individual small farmer, businessman, and trader. He it was who created the wealth and provided the sinews that made the Empire. When this class, for whatever reason, was forced out of existence, the "grandeur that was Rome" quickly faded.

Beginning with the third century, the power of Rome began to wane. Slowly but surely the ordered, progressive life in a well-tended countryside and in hundreds of cities with fine public buildings, temples, and homes was undermined by anarchy, insecurity, and discord at home and by successive waves of barbarians from the north and east. Imperial edicts proved a poor substitute for the individual efforts of free men. Thus the structure of the Empire was weakened from within and rendered highly vulnerable to attack by tribes of vandals which gloried only in destruction, murder, and rapine. So thoroughly did they carry out their mission of destruction that by the seventh century a once productive countryside had largely reverted to waste, the once proud cities were in ruins, and the population cut in half. There was barely enough courage and initiative left to start the long, tedious process of rebuilding, which was to consume the next 600 or 700 years. The effect on livestock breeding was particularly severe. Herds and flocks were wantonly destroyed and their half-starved remnants turned back to a state of nature.

Grecian Agriculture and Animal Husbandry.—Before the time of Alexander, agriculture and stockbreeding were one of the chief sources of wealth in Greece and her colonies. Their stables and byres contained horses, cattle, sheep, swine, and goats, which provided food, clothing, milk, and power. These early Greeks also kept bees, and the poultry yard contained geese, ducks, guinea fowl, and pigeons as well as hens. These people also consumed various and sundry products of the field, grains, vegetables, and fruits, and their banquets and religious ceremonies called for the liberal use of wine. In the early days of Greece, the standard of value was measured in terms of cattle, and among the prizes suggested by Achilles for the funeral games in honor of Patroclus were, besides mares and mules, a tripod valued at 12 oxen and a slave girl valued at 4 oxen. There was considerable barter involving the exchange of cattle for metals. The Greek poems of the period contain many references to wealth reckoned in terms of flocks and herds, just as in later Roman times the word for money, *pecunia*, was derived from *pecus*, cattle. The earliest known Greek coins date from the seventh century B.C.

Economic activity at this time was mainly agricultural and pastoral, pursuits which provided most of the wealth. Through the period from

the eleventh to the fourth centuries B.C., some improvements in details of agriculture and animal husbandry are recorded, but there was no radical change in agricultural equipment or methods and no evidence of any marked development in stockbreeding practices. Much of the work was done by slaves, though there were also individual farmers who owned and operated their farms as well as some farms that were run by hired labor.

FIG. 10.—Statuette of Greek horse in bronze, fifth century B.C. (*Courtesy of The Metropolitan Museum of Art.*)

When Alexander of Macedon led the Greeks to the conquest of Asia Minor and Egypt, a new and rich agricultural economy fell under Greek domination. Here they found a flourishing livestock industry: 30,000 mares with 300 stallions in one stud in Syria, large herds of camels farther east between Syria and the Euphrates Valley. Great herds of oxen and horses were found in the well-watered districts from the Mediterranean to the Black Sea with flocks of sheep in the higher plateaus. Even greater agricultural and livestock wealth awaited them in Egypt in spite of the misrule of the Persians during the two preceding centuries. Egypt now became the granary of the Mediterranean world in addition to supplying countless other vegetable and aromatic products as well as fruits.

Livestock too abounded in Egypt: horses, cattle, sheep, goats, poultry, of various sorts, and the real beast of burden, man's fellow worker in the fields and on the roads, the lowly ass. In addition Egypt supplied all sorts of wild game, gazelle, antelope, wild ox, goat, hare, hyena, lion, hippopotamus, crocodile, and various waterfowl. Thus a whole new world was opened up by the Greek conquest. There were huge temple properties and royal domains in both Asia Minor and Egypt, the former apparently worked by slaves and the latter by royal farmers, who were somewhat of the nature of serfs and tenants, as well as by salaried workers. In addition, there were large estates worked by tenants and

Fig. 11.—Wall painting of Egyptian bull during XVIII dynasty, about 1400 B.C. (*Courtesy of The Metropolitan Museum of Art.*)

probably some small, free landholders. Greek agriculture and animal husbandry certainly took on a greater diversity during the centuries that saw Greek influence spread to Asia Minor, Syria, and Africa, but there is little evidence of any marked improvements in the techniques of either. Beneficial variations were no doubt seized upon and in some cases maintained or increased, but the general level of accomplishment in stockbreeding remained about where it had been.

Oriental Agriculture and Animal Husbandry.—Colored drawings on the walls of the tombs clustered around the Pyramids of Giza depict the life of the people who lived in Egypt about 3000 B.C. The lord of the estate is pictured looking out over his fields, the oldest agricultural scene now

known. Cattle are shown being used to pull a crude wooden plow; others are shown grazing in pasture and still others being milked (after their hind legs had been tied to prevent kicking). Donkeys too are much in evidence, but the horse was apparently unknown to the Egyptian at this time, not appearing there until about 1700 B.C. At the Plain of Shinar, later known as Babylon, carvings and drawings from about the same time show oxen at the plow, sheep and goats at pasture, and donkeys pulling wheeled carts and chariots, the wheel appearing here for the first time. Horses made their appearance in Western civilization about 200 B.C. when they were brought to Babylon by the conquering mountain

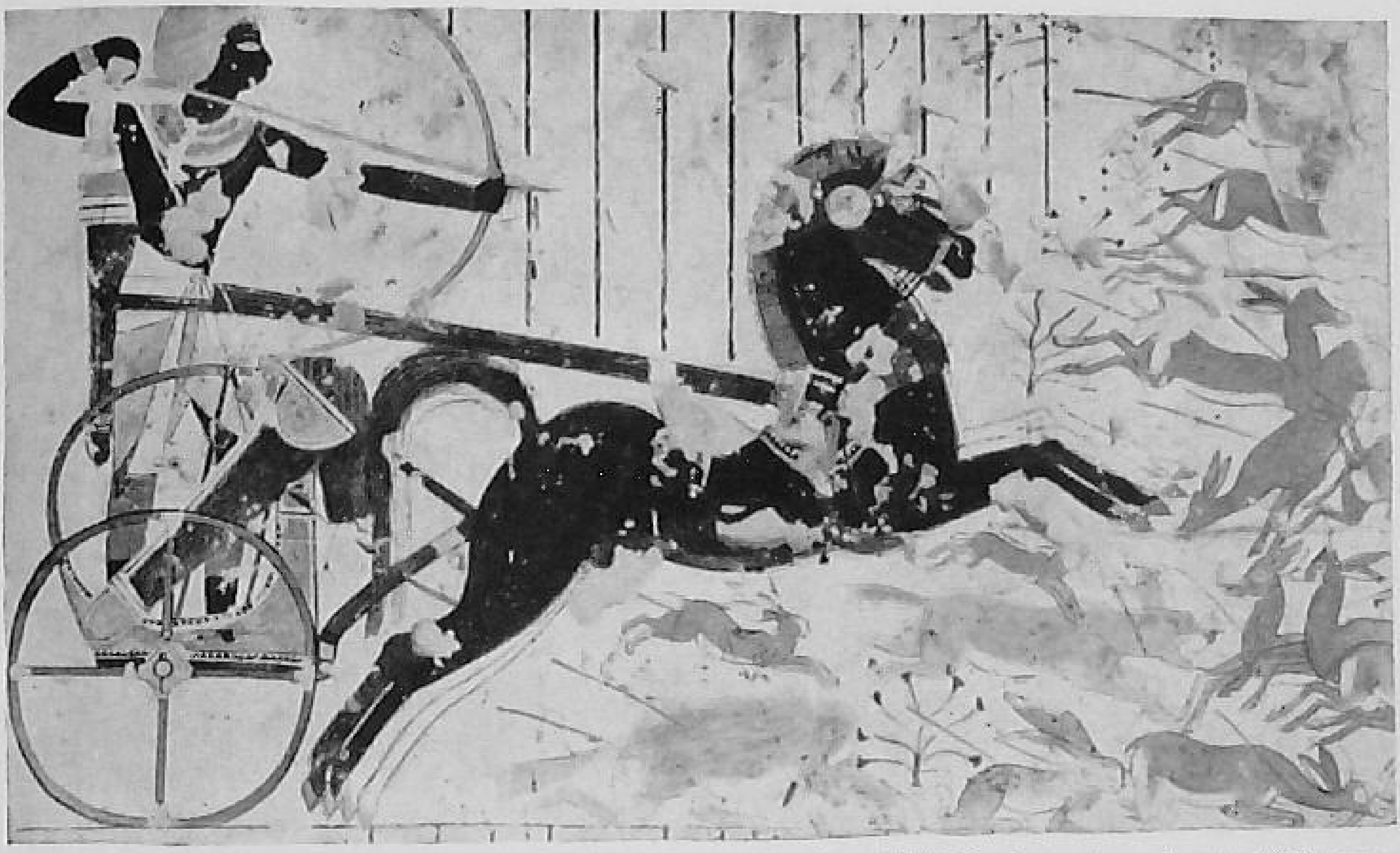

FIG. 12.—Wall painting of Egyptian hunter during XVIII dynasty, about 1400 B.C. (*Courtesy of The Metropolitan Museum of Art.*)

Kassites, who in turn had gotten the domesticated horse from tribes to the north and east. To the north of Babylon was another early civilization, the Assyrian, with its capital at Nineveh. These people too had herds of oxen, sheep, and goats and used donkeys for draft purposes. They also had domesticated horses which, together with their weapons of iron, they used very effectively in their conquests of neighboring regions. The peoples who made the Babylonian, Assyrian, and Chaldean empires came largely from the grassland fringes of the Arabian desert.

In the north was a second fount of nomadic conquerors located in the grasslands stretching from the lower Danube along the north side of the Black Sea through southern Russia and into Asia. This was a white race called Indo-European, and most of the people who will read this book are their descendants. Their original home was the grassy steppe east and

northeast of the Caspian Sea. They were nomadic tribes following their flocks and herds on horseback and using horses for draft. These people were the ancestors of the Greeks and Romans and of most of the peoples of Western Europe and America. Their language group is Aryan, which includes English, German, Latin, Greek, old Persian, and East Indian, although these people themselves were without writing. The Medes and the Persians were but the Eastern wing of this movement of original Northern nomads.

Here the historical record fades out. What preceded it in the field of agriculture and animal husbandry can only be surmised from occasional relics. This historical record we have traced backward from the present, a period covering about 5,000 years. We have noted some progress, but the tempo of change was very slow. We are perhaps justified in assuming that the period from the earliest domestication of animals up to this beginning of the historical record occupied a much longer time.

Summary.—We have tried in this chapter to start from the known facts about our livestock situation of today and trace it backward to its historical beginnings. In these few pages we have covered 5,000 years of man's struggle from barbarism to a certain state of civilization. Much was accomplished, but a vast deal more still remains to be done. Without any sure knowledge, except what he could observe in the gross, man has made tremendous strides forward in breeding better livestock, aided materially, of course, by better housing and management and especially by better feeding. For marked progress in animal breeding, we need knowledge of principles, ideals, and good feeds together with peace or at least freedom from invasion. All these except the first were finally present in England during the eighteenth century, and it was there and then that the foundations of our modern breeds were laid.

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CHAPTER II

EARLY MAN AND ANIMAL DOMESTICATION

Man is a late arrival on the planet Earth. When he arrived, he found the earth already inhabited by myriad forms of living things. He was apparently just another in a long series of creations extending back for hundreds of millions of years to the beginning of life, just another manifestation of the great stream of life that far transcends man's own immediate interests. Before him, in time, had arrived many of the other mammals as well as the birds, reptiles, amphibia, fish, and a whole host of invertebrate forms.

It is estimated that life has existed on this planet for about 1,200 million years. Up to about 500 million years ago, the only animal forms were creatures without backbones, the invertebrates. The vertebrates, animals with backbones and an internal skeleton, appeared about 480 million years ago, the first land-living forms about 350 million years ago, the mammals about 160 million years ago, *Homo sapiens* (wise man) about 25,000 years ago, and we have something of a historical record of his doings for about 5,000 years.

The record yielding the above facts is written in the rocks of the earth's crust. The time intervals are calculated on the basis of the rate of breakdown of certain rare minerals and for more recent periods by counting the annual glacial varves. Even the ancients must have sensed something of the span of time when they wrote "A thousand years in Thy sight are but as yesterday when it is past."[1] In these trying times facts such as the above should give us new courage. In a ridiculously short span of time man has made tremendous strides forward. To say, as is sometimes done, that human nature does not change is but to show one's ignorance of the facts. Present man is probably very different intellectually, morally, and spiritually from his forebears of 50,000 years ago. In a few hundred years, recent man has come largely to understand and to be the master of his natural world. True, the much more difficult task of becoming master of himself yet remains, but in the light of the accomplishments of the stream of life over the past billion years this does not seem to be an impossible task.

The first skeleton of "modern" man appears in the geological record

[1] Psalm 90: 4.

about 25,000 years ago. Starting with *Pithecanthropus erectus* (walking ape man), who dates back from ½ to 1 million years, an incomplete and rather sketchy series of prehuman forms runs on down and finally emerges as modern man. Man is included in the Primates, a group of animals comprising the lemurs, monkeys, apes, and man. This does not mean that man has descended from monkeys but probably that man, monkeys, and the great apes are all offshoots of a common progenitor whose identity is still uncertain. The apes, therefore, are our cousins and not our direct ancestors.

The primates as a class are not of very recent origin, for fossil remains of the lemurs are known from the Oligocene and Eocene periods, *i.e.*, 35 to 55 million years ago. It is impossible to say when the stock that was eventually to form man split off from the parent stock, though it is believed that both man and the modern apes are descendants of a common progenitor in the Cenozoic period. Neither is it known where, geographically, the split occurred, though either Asia or Africa seems the most probable, or whether there was one split or several in scattered localities.

The close relationship between the great apes and man is attested by the striking similarities in all their physical characteristics. One can easily point out differences between a gorilla and a man, but a detailed study would show very much more similarity than difference between these species. The monkeys and apes excel in certain respects—man in others. The most striking variations in man are, of course, the upright gait, which frees the hand to become a grasping, tool-making and -using organ, and the development of the brain. Man's brain is the finest creation of the evolutionary process and is not to be thought of as something supernatural, miraculous, or of sudden appearance. It is a slow, progressive development of evolution and still manifests a wide range of variation.

Early Forerunners of Man. *Pithecanthropus erectus.*—This, the ape man of Java, was discovered by Dr. E. Dubois of Holland on the island of Java in 1891. The find was made 45 ft. below the present level of the terrain in association with 27 different varieties mainly of extinct mammals but including the deer, boar, elephant, and hippopotamus. The find consisted of a skull cap, a left thighbone, two upper molar teeth, a lower premolar, and a fragment of a lower jaw and is generally dated as of early to middle Pleistocene Age. The skull cap is thick-walled and has a cranial capacity of about 900 cc., which is somewhat below the lower limit of present-day human skull capacity, and the brain gives evidence of being closer in form to the human than to the ape. The skull cap indicates a low cranial vault and a narrow receding forehead, and it has a

TABLE 7.—COSMIC OR ASTRONOMIC TIME CHART*

Eras	Periods	Time, years	Characteristic life
Psychozoic...	Recent	25,000	Man
Cenozoic, 4 per cent	Pleistocene	1,000,000	Ice Age
	Pliocene	7,000,000	Emergence of man
	Miocene	19,000,000	Culmination of mammals
	Oligocene	35,000,000	Modern mammals dominant
	Eocene	55,000,000	Archaic mammals, first horse
Mesozoic, 11 per cent	Cretaceous	95,000,000	First grasses; Culmination of reptiles
	Comanchian	120,000,000	First flowering plants; Giant reptiles, dinosaurs
	Jurassic	155,000,000	First birds, first mammals; First modern trees
	Triassic	190,000,000	Rise of dinosaurs
Palaeozoic, 30 per cent	Permian	215,000,000	Rise of reptiles
	Pennsylvanian	250,000,000	Rise of insects; Ferns and seed ferns
	Tennessean	275,000,000	Rise of sharks
	Mississippian	300,000,000	Rise of echinoderms
	Devonian	350,000,000	First land plants; First land animals
	Silurian	390,000,000	First lungfishes; First scorpions
	Cincinnatian	425,000,000	First corals
	Ordovician	480,000,000	First armored fishes
	Canadian	490,000,000	
	Ozarkian	505,000,000	Trilobites dominant
	Acadian	525,000,000	First shellfish
	Taconic	550,000,000	First known marine fauna
Proterozoic, 25 per cent.	....	....	Primitive invertebrates
Archaeozoic, 30 per cent.	....	1,800,000,000	Earliest life

* LOOMIS, F. B., "The Evolution of the Horse," p. 24, Marshall Jones Co., Boston, 1926.

very well-developed supraorbital ridge that is suggestive of the great African apes. The thighbone indicates an upright, bipedal posture, and, judging from this bone, the creature stood about 5½ ft. in height. The two molar teeth are now thought to be those of an orang, although another much more humanlike tooth was found in the same stratum sometime later, which, if it really belonged to Pithecanthropus, adds another to this creature's manlike characteristics.

Whether Pithecanthropus was a direct ancestor (missing link) or just a collateral relative is still a question. At any rate, he still remains the lowest known member of the family Hominidae. Since no tools or artifacts were found associated with these bones, we can guess nothing as to the degree of culture that members of this race had attained, though it seems safe to assume that any culture they may have possessed was of a very primitive type.

Another find (by Dr. G. H. R. von Koenigswalde) was made in Java in 1936. This was the skull of an infant about one to two years of age, though the teeth, which would give the best indication as to age, were not found. The capacity and characteristics of this skull seem to place it in the Pithecanthropus group of the lower to middle Pleistocene, although some authorities would designate it as a skull of an infant Solo man of upper Pleistocene age. In 1937, Dr. von Koenigswalde found an adult Pithecanthropus skull in Java including four teeth of undoubted human form though of great size. This skull has an estimated capacity of about 750 cc. More recently a fourth specimen of Pithecanthropus was found of the same general type.

Sinanthropus pekinensis (*Peking Man*).—The finding of human teeth in cave deposits near Peking, China, in 1926 and 1927 led to further search in this region for human remains. The search was rewarded in 1929 when Dr. W. C. Pei of China found a nearly complete skull. Another skull was found in 1930, and since that time many fragmentary skulls, teeth, and parts of skeletons have been discovered. In 1936, three more skulls were discovered, including some of the facial bones. The first skull had a cranial capacity of something over 900 cc., and the capacity of the second was somewhat greater. The three latter skulls have capacities of 1,200, 1,100, and 1,050 cc., the last probably a female.

The general form of these skulls is similar to that of Pithecanthropus, the teeth are of human type and larger than those of recent man though there is still no chin. Associated animal fossils indicate that these men lived at about the same time as the Java man, *viz.*, during the middle Pleistocene; *i.e.*, 500,000 to 1½ million years ago. It seems established that the Peking man used fire and had crude implements and tools made of chipped stone or the bones of animals. The greater brain capacity

and manlike teeth perhaps place Sinanthropus a little higher in the scale than Pithecanthropus.

Eoanthropus dawsoni (*Piltdown Man*).—This discovery was made by Charles Dawson in 1911–1912. It consisted of several fragments of a human skull, much like that of a modern except for its excessive thickness of bone, and, in close proximity, the right half of a lower jaw containing two molar teeth. This portion of jaw is very similar to that of a chimpanzee, a creature, however, never found fossilized in England. Later finds, near Piltdown, of skull fragments and teeth tend to confirm the once-doubted fact that the skull and jaw belonged originally to the same creature. The cranial capacity seems to be about 1,200 cc., and the forehead not only lacked the supraorbital ridge but was quite vertical. The

FIG. 13.—Prehistoric man; Pithecanthropus, Piltdown, Neanderthal, Cro-Magnon. (*Courtesy of The American Museum of Natural History.*)

apelike lower jaw has no chin but its jaw socket is formed as in *Homo sapiens*. A chipped flint and a large bone implement were found in the deposit that is generally accepted as being of early Pleistocene. These fossils have caused a great deal of argument among anthropologists, and it is still not clear where the Piltdown man fits in the general scheme of man's forerunners.

Homo heidelbergensis (*Heidelberg Man*).—This find, of a lower jaw, was made by Professor Schoetensach at Mauer, near Heidelberg, Germany, in 1907 in river sand 79 ft. below the present surface in a stratum that had yielded many bones of Pleistocene animals. This individual is thought to have lived 150,000 to 300,000 years ago. The jaw, while very heavy, has teeth that are entirely human. No artifacts were found associated with this jaw, so that nothing can be guessed as to the cultural status prevailing during his time. Again it is impossible to assign a

definite place to this undoubted forerunner of man. It should be noticed that we have herewith used for the first time the genus name for man—*Homo*. That is to say *heidelbergensis* appears human enough to be placed in the same genus with present man—but he is not yet called *sapiens* (wise).

Homo neanderthalensis (*Neanderthal Man*).—We now reach a type concerning which something more definite may be said. First of all, Neanderthal man spread over the continent of Europe, into the Channel islands, and into Palestine. He had a well-defined flint-tool industry, used fire, probably buried his dead, lived contemporaneously with the reindeer, wild horse, cave bear, and woolly mammoth during a time extending from 200,000 down to 25,000 years ago.

The first known Neanderthal skull was found in 1848 at Gibraltar, though it was not recognized as such or studied until 1906. It was that of a female with a brain capacity of about 1,300 cc. The discovery at Neanderthal occurred in 1856. This skull has a very low vault, heavy supraorbital ridges, and many unusual features in the arm and leg bones.

One of the most complete skeletons thus far discovered was found at the cave of La Chapelle-aux-Saints in France in 1908. This was an almost complete skeleton which had been buried in the floor of the cave. It has been studied in complete detail by Prof. M. Boule of Paris. Other Neanderthal skeletons or parts thereof have been discovered in various parts of France, Germany, Italy, Yugoslavia, Palestine, and in the Crimean Peninsula on the Black Sea. As would be expected, there is considerable variation in these skeletons, but no basis as yet exists for breaking *neanderthalensis* up into several "races."

The general type is that of a short, heavy-boned man. The brain capacity, both sexes considered, varies from about 1,100 to 1,600 cc. The head is long but does not extend very high above the ears. There is a huge supraorbital ridge, a retreating forehead, large eye orbits, a wide and rather prominent (not flat) nose, long upper lip, and little or no chin. The forearm and shin are short in comparison with the arm and thigh, the thumb is opposable, the big toe not (just as in modern man), and there are several apelike characters about the feet. *Neanderthalensis* probably walked more uprightly than many artists have represented.

This hurried survey of man's forerunners has brought us down to the last phase of the Old Stone or early stages of the New Stone Age. Our last representation of preman, *neanderthalensis*, lived during the Old Stone or Paleolithic Age. He had come a long way from Pithecanthropus in physical beauty and probably had progressed mentally as well. So far as is known, he was still a hunter and food gatherer. He had, however, learned to make and use fire, which, together with his earlier tool-

making, was an important step in his emancipation from environmental bondage. No one knows how he lived, but undoubtedly it was a rather precarious existence—killing or catching enough game to piece out the roots, berries, and seeds which he could find, and all the time in danger himself of being devoured. To learn how best to hunt or fish, which foods would nourish and which kill was a long slow process; but, when once learned, it was undoubtedly quickly absorbed into the cultural tradition and passed along to each new generation. Considerable skill, courage, and cooperative effort were undoubtedly needed to hunt the mammoth, bison, wild horse, and reindeer that roamed over the steppes and plains. These hunters undoubtedly followed the herds as they migrated, north to Russia and Siberia—south to the Danube basin. We get a glimpse of the fauna of the upper Paleolithic through the fact that these peoples carved animals in stone or ivory, drew and painted them on the walls of their caves, and modeled them in clay.

These hunters and food gatherers were content to live on what nature provided though undoubtedly they progressively improved their methods of seizing what nature offered. The first great forward step—that from food gathering to food producing—had to await the arrival of a more ambitious, more intelligent man than *H. neanderthalensis* and the wait was not to be long.

Homo sapiens (*Modern Man*).—Where *sapiens* came from and when he arrived is not definitely known. We see *neanderthalensis* surviving for perhaps a few thousand years following the last glacial period, say until 25,000 years ago. Then he seems suddenly to have disappeared and to have been replaced by *H. sapiens*. This occurred in the last stages of the Paleolithic, which merged with the Neolithic or New Stone Age, about 10,000 years ago. Speculations regarding the origin of early *sapiens* and his relation to the modern races of man have been numerous; actual data in the case are about negligible. Did he (*i.e.*, *H. sapiens*) come in from Asia or from Africa to blend with or totally supplant *neanderthalensis?* Or did the latter evolve into *sapiens?* All we can do at present is to ask the questions and hope the future may provide an answer.

The "Grimaldi Race."—Near Monaco on the Mediterranean coast in the so-called "Grimaldi caves" there were discovered in 1901 two skeletons, one of a woman, the other of a fourteen-year-old boy. These skeletons are of a distinct type. Both of them were about 5 ft., 2 or 3 in. tall. The leg and arm bones and more particularly the head and facial bones are strongly suggestive of negroid characteristics. They have caused considerable argument in anthropological quarters, but the bulk of opinion now inclines to the belief that they were not representative

of a distinct "Grimaldi race" but rather an early and primitive example of a late Paleolithic stock—the Cro-Magnon.

Cro-Magnon Man.—This was the name assigned to five skeletons that were found buried in the Cro-Magnon rock shelter in the Dordogne, France, in 1868. Other finds of this type have been made in various parts of Western Europe. This was probably a fairly tall race, with long heads, a high vertical forehead, short, broad face, prominent nose and chin. The shin and forearm were long in comparison with thigh and upper arm. This type of man, living in the late Paleolithic or Old Stone Age, had a well-developed culture. Certainly they made quantities of flint and bone tools and were excellent artists and sculptors. Their origin is not yet known, and it is believed that they intermingled with other stocks, and perhaps traces of them are still to be found in men living today. What a fascinating thing it would be if you and I could trace just one line of our pedigree back to the year, say, 13,000 B.C. just to make the wish moderate!

FIG. 14.—Neolithic man of the Campignian Stage. Mural painting by Charles R. Knight. (*Courtesy of The American Museum of Natural History.*)

Several other fossil remains of man have been discovered, *viz.*, Wadjak man (Dr. E. Dubois) and Solo man (W. F. F. Opperworth) from Asia; Rhodesian man (A. S. Woodward) and Boskop man (Dr. R. Broom) from Africa. But these, together with several other finds, it has not been possible to place with any degree of satisfaction in the general pedigree of mankind or his collaterals.

In all this length of time, from perhaps 1 million years ago down to 10,000 or 12,000 years ago, man traveled his difficult way without the aid of a settled agriculture and animal husbandry. The wonder is of course that he survived at all. He lived side by side with many other

mammals, some extant, some extinct. Probably for vast periods of time man has used animals for food and their skins for clothing and shelter. This Paleolithic hunting stage has persisted in some places right down relatively to the present, *e.g.*, in Australia, Africa, and America.

Hunting Stage.—The exact times and places of the domestication of plants are, of course, unknown, and there has been much debate as to whether agriculture preceded or followed the domestication of animals. Opinion at the present leans to the following sequence: first hunting; then a hoe or hand culture, then animal domestication; then agriculture or an animal-power culture; and, finally, the extensive development of herds and flocks into a pastoral culture, although herding may have preceded agriculture in certain areas.

Certainly, we are justified in assuming the hunting stage to have preceded all forms of agriculture or animal husbandry. Man lived at this time on what roots, berries, and seeds he could find and on such insects, animals, and fish as he could catch. Gradually, we can imagine, he improved his techniques for finding sources of food and utilizing these natural sources so that they would return a better yield. Likewise his techniques of hunting and fishing improved. He learned to trap and spear fish, to make ingenious traps and pits into which animals could be lured or driven, and to disguise himself under the skin or hide of the animal he was hunting in order to permit a closer approach. In this stage it seems safe to assume that the men generally provided the meat portion of the diet, while the women largely supplied the vegetable products. This has led to the assumption that women were probably the real instigators of agriculture.

During this stage of man's development, he had to make the best of his own particular environment. Some regions, no doubt, provided ample game and fish and little food of a vegetable nature, while in some other regions the reverse situation was encountered. Man being omnivorous, this type of enforced adaptation would present no very great difficulties. There were undoubtedly wide variations during this early hunting or food-gathering stage of man's existence. It has sometimes been assumed that these hunters were extensive roamers, but it seems more logical to think of each group confining itself to a relatively small area where they would not come into direct conflict with other groups. Under these conditions, children are a distinct liability, and it seems probable that groups increased at a very slow rate.

Early Plant Culture.—Somewhere man took his first decisive step that was eventually destined to lead him up out of savagery. He had been utilizing such vegetable products as nature had provided him just as he found them. Now, however, he begins to try to control this source

of sustenance. He takes wild grasses, wheat, rye, oats, corn, and various bulbs, tubers, and trees and tries in his crude way to control and assist their growth by scratching and preparing the soil, removing weeds, protecting them from animals, and, finally, probably after seeing their more luxuriant growth on dung and refuse heaps, by actually feeding the plants. Thus in many parts of the world and under a great variety of conditions our grains, tubers, and fruits were brought under man's conscious control. Later the creation of one region found its way to a new locality where it sometimes was added to the local accomplishments, and sometimes it totally superseded and displaced the old. This momentous step in man's history occurred after the last glacial period, probably in the early part of the Neolithic.

Closely associated with agriculture was the art of storing and preserving food. Just when it developed is not proved, though man had no doubt been observing similar activities on the part of animals for a long time. In fact, to have survived at all it seems that man must early have learned how to store up food to tide over periods of shortage. At any rate, after the domestication of plants, there would be more to preserve, and any process that causes man to take forethought is a considerable stimulus to civilization, for it embraces the feature of man's nature which more than any other thing differentiates him from other animal forms. This earliest stage of plant culture (sometimes called "hoe culture") does not imply the use of domestic animals.

The Metal Ages.—The paleolithic, or Old Stone Age, with its crude stone and bone implements, gradually merged into the Neolithic, or New Stone Age, with its polished stone and bone tools and implements, about 10,000 years ago. Sometime during the Paleolithic Age man learned to use fire, but he had no agriculture and probably no domestic animals except perhaps the dog. Sometime during the Neolithic, agriculture and animal domestication came into being, and these peoples learned how to build shelters of wood.

The ancient stone ages were finally superseded by the various ages of metals. Metals reached Southeastern Europe soon after 3000 B.C. but did not penetrate to Northern and Western Europe until nearly 2000 B.C. The first metals used were copper and its alloy of tin, bronze. This was followed about 1000 B.C. by the Iron Age. Thus the three great ages of stone, bronze, and iron followed and blended into each other, although their dates in different localities may have differed by a thousand years or more, so that Bronze Age here may have been Iron Age there. With the development of better and more durable tools, the improvement of agricultural and animal-husbandry practices, civilization developed new impetus.

Domestication of Animals.—Just when the domestication of animals began is unknown; it certainly was long before there was any thought of, or means for, recording historical data. Domestication very likely began at the end of the Old Stone Age and received decided impetus during the New Stone Age. Each domestic animal has had a rather restricted and humble origin, yet through constant selection for one or another character all of the multifarious forms have evolved—some useful, some ornamental, some having both qualities, and some neither. Selection always has been and always will be the key to animal breeding.

Although the exact beginning of the domestication of animals is unknown, it seems logical to infer that, with the possible exception of the dog, it arose when man ceased to be purely a hunter and adopted a more or less settled mode of living. This new mode of living demanded that food be close at hand. This in turn necessitated plant and animal culture. From that remote time to the present, man has been growing plants and animals, selecting promising variations, and eventually establishing pure strains of plants and pure breeds of animals. Plants and animals have both reached a stage of marked efficiency through long periods of breeding. Superior animals were no doubt developed by each of the ancient civilizations and suffered retrogression with the decline of the civilization of which such development was a product.

Though its exact time, origin, and mechanism are, and perhaps always will remain, wholly unknown, animal domestication continues to be a lively field for discussion. It is true, also, that if we knew the pedigrees of all our animals back to the very origin of the mammals, we might not be any better fitted to breed good livestock today. Still we like to try to piece the scattered details together into a theory that seems to have some degree of plausibility. Of one thing we can probably be certain, *viz.*, that Neolithic man did not hatch full-blown the idea that animals could help him in his difficult struggle for existence. This is undoubtedly true for the reason that at that time swine did not fatten rapidly, sheep produced no wool, cows gave only enough milk for their calves, and the wild horse was probably quite intractable. True, animals have been of untold benefit to man, but their potentialities have been revealed bit by bit over a period of thousands of years.

All our larger farm animals belong to one order, the ungulates or hoofed animals; cattle, sheep, and goats to one smaller group, Pecora. Why did man select just the animals which he did for domestication? Did he try to domesticate many others and fail? True, when we list all man's domestic animals, we have quite an array—horse, ass, cattle,

yak, water buffalo, sheep, goat, swine, camel, llama, elephant, dog, cat, reindeer, guinea pig, rabbit, rat, mouse, poultry, turkey, duck, goose, guinea, silkworm, honeybee—and who knows that other conquests will be made in the future?

For successful domestication, of course, animals had to have the proclivity of breeding in captivity as well as a certain degree of tractability. The dog has had a varied history under domestication. It is thought that he started out as a scavenger living on the outskirts of man's settlements. From this he grew to be a pet, companion, herder, and protector, an ally in the chase, a source of food, clothing, and tractive power. No other animal has filled so many human needs as the dog. The reindeer, on the other hand, probably owes his domesticity to his fondness for human urine, which he apparently considers quite a delicacy as a source of salt. Many fowl were apparently domesticated for magic and religious purposes and at the time laid very few eggs. Some tribes domesticated the pigeon just because they liked its looks. In other words, many animals have been domesticated for a variety of reasons, none of which was practical. Even today some native tribes keep vast herds of cattle merely for the pleasure of possession.

On the contrary, travel in the desert without the aid of the camel or in the arctic without the reindeer or dog would have been difficult, if not impossible, as these animals often provide milk as well as transportation and often feed themselves in the bargain. On the contrary, the Egyptians made no use of their hogs and sheep as food, and the Chinese used cattle for thousands of years as beasts of burden but never used their milk.

It seems probable that there were several centers of domestication, but where they were is not known. It is generally accepted that the dog was domesticated, probably from the wolf with whom he will still mate successfully, in the late Paleolithic or early Neolithic. There is no safe or accepted chronological order for the domestication of the larger farm animals. Drawings of cattle, sheep, hogs, and donkeys occur in Egyptian writings dating back to 3000 or 4000 B.C. The horse is mentioned in Babylonian writing about 2300 B.C. and appears in Egypt about 1700 B.C. Camels are mentioned in Mesopotamia in 1100 B.C. How much earlier the actual domestication may have taken place is, of course, unknown.

Influence of Domestication on Civilization.—Many factors have influenced the development of civilization, such as the development of speech and writing, the use of tools, the discovery of fire, and the harnessing of steam and electricity. Along with these we must also place the

development of agriculture and the domestication of animals. Certain it is that without agriculture and domestic animals man would of necessity still be a nomad and hunter. The domestication of plants and animals furnished the magic "open sesame" that beckoned man out of his dirty, pinched cave to establish a glorious countryside and later to build great cities. By lifting physical labor from his shoulders, it also freed his mind for the development of science as well as for the contemplation of the beautiful. Domestic animals have long been man's most dependable friends and strongest allies in his task of conquering the world in which he lives. All the energy on this planet originates in the sun and the majority of it is stored here in forms that man cannot use directly, *e.g.*, grass, straw, stalks, etc. Domestic animals are merely machines that man has adapted to convert these stores of otherwise unusable energy into useful forms.

Before he domesticated plants and animals, man was a savage motivated largely by selfishness, with little incentive to provide for the future. Like little children the savage is inclined not to look beyond his immediate interests and pleasures. He lives in the present with little thought for the future. Coming into possession of animals changed this, for their future wants must be foreseen and provided for if they are to be of any real service. Flocks and herds must also have had a marked tendency to broaden the sympathies of the savage—in short, to lead him out of savagery and start him on his journey toward civilization. Our civilization is greatly indebted to domestic animals, though for the most part we are inclined to take their contribution as a matter of course. There is no instance of any race or tribe of man having reached a high state of civilization without the aid of domestic animals, and the leading and conquering nations have always been far advanced in the arts of husbandry. Domesticated animals have nourished as well as reinforced man's sinews, quickened his mind, and broadened his sympathies, so that it is hardly too much to say that the development of civilization had to wait upon the domestication of animals, even though civilization may always have gotten its start in grasslands or centers of grain culture which could be carried out by unaided human labor.

The Dog.—Available evidence indicates that the dog was the first animal domesticated by man, to be followed next by the even-toed ungulates, or artiodactyls, cattle, sheep, and swine, and, finally, by a representative of the perissodactyls, or odd-toed ungulates, the horse. Besides being first in time the dog still holds first place as man's companion. Cuvier, the great French naturalist, wrote:

> The dog is the most complete, the most remarkable, and the most useful conquest ever made by man. Every species has become our property; each indi-

vidual is altogether devoted to his master, assumes his manners, knows and defends his goods, and remains attached to him until death; and all this proceeds neither from want nor constraint, but solely from true gratitude and friendship. The swiftness, the strength, and the scent of the dog have created for man a powerful ally against other animals and were, perhaps, necessary to the establishment of society. He is the only animal which has followed man through every region of the earth.

The following portion of a poem by Walter Scott depicting the faithfulness of the dog was inspired by the story of a young man who lost his life by falling from one of the precipices of Mt. Helvellyn. Three months later his remains were discovered at the bottom of a ravine, and his faithful dog, almost a skeleton, still guarding them.

> Darkgreen was the spot: mid the brown mountain heather
> Where the pilgrim of nature lay stretched in decay;
> Like the corpse of an outcast, abandoned to weather,
> Till the mountain winds wasted the tenantless clay;
> Nor yet quite deserted, though lonely extended,
> For, faithful in death, his mute favorite attended,
> The much loved remains of her master defended
> And chased the hill-fox and the raven away.
> How long didst thou think that his silence was slumber?
> When the wind waved his garments how oft didst thou start?
> How many long days and long weeks didst thou number
> Ere he faded before thee, the friend of thy heart?

The dog, an unguiculate, *i.e.*, having claws or nails rather than hoofs (ungulate), belongs to the order of mammals known as the Carnivora, meaning flesh eaters. There are two suborders of the Carnivora, the aquatic carnivores, or Pinnepedia, such as the seals and walruses, and the land carnivores, or Fissipedia, including the dogs, cats, bears, etc. The Carnivora have small incisor and large canine teeth with the anterior molars or premolars usually modified for shearing. The Fissipedia include the following families, the Viverridae (genets), Felidae (cats), Hyaenidae (hyenas), Mustelidae (weasels), Procyonidae (raccoons), Ursidae (bears), Protelidae (earth wolves), and the Canidae (dogs, wolves, etc.).

The chief genus of the family Canidae is that called Canis. In this genus are to be found modern domesticated dogs, *Canis familiaris;* as well as the wolves, *C. lupus*, etc.; the jackals, *C. aureus*, etc.; and the foxes, *C. decussatus*, etc. The chief differences between these four species of Canis lie in the shape of the eye and its pupil. The dog, the wolf, and the jackal are interfertile, and their gestation periods are of similar

length. The dog has five toes on the front feet and four on the hind feet. The typical dentition in this family is:

Incisors	Canines	Premolars	Molars
$\frac{3}{3}$	$\frac{1}{1}$	$\frac{4}{4}$	$\frac{3}{3}$

Origin and Domestication of the Dog.—The ancient ancestry of the dog is very little known. Owing to the closeness of the anatomical and skeletal features of the dog and the wolf, it is quite generally stated

Fig. 15.—St. Bernard (Hercuveen Chum) and Chihuahuas (La Rex Doll Pon Pon and La Rex Doll Snowflake), the results of nature's variation and man's selection. (*Underwood and Underwood.*)

that the dog is an offshoot of the wolf tribe. Possibly savage hunters captured wolf puppies and took them home to amuse the children, and in this way through the course of time the wolf gradually lost his ferocity and aloofness and learned how to bark joyously at his master's approach.

The jackal of the Old World, a smaller, more yellowish wild dog and much less ferocious than the wolf, is believed by some to be the progenitor of the dog. This strain is also much more easily tamed than is the wolf. Some also have suggested that the dog arose as a result of a cross between wolves and jackals. Nothing definite, however, is known regarding the dog's progenitors.

Various breeds of dogs existed during the Roman classical period, and some of these are preserved in sculpture. Dogs are also represented on the Egyptian monuments as far back as 3400 B.C. Skeletal remains of a canine animal are embedded in the Danish middens of the Neolithic, or New Stone Age. The dog has, therefore, been in existence for at least 5,000 to 8,000 years.

The dog may first have served as a source of food for ancient men in times of famine. This in itself would have been a powerful selective agency, as the least valuable would have been the first sacrificed. At a later period, before the time of the advent of agriculture and a more or less settled mode of existence, he no doubt became an invaluable ally in the chase. Later still, certain strains were used for draft as are the Eskimos and other dogs of today. Through it all, the dog has continued to grow in man's affection no doubt because of his sagacity and faithfulness and also because more than any other animal the dog is both capable and desirous of returning any evidence of affection.

There are now recognized six distinct groups of dogs, *viz.*, the greyhound, hound, mastiff, spaniel, terrier, and wolflike. Mason's "Dogs of All Nations" lists 183 breeds of dogs from 39 countries. The variations in the different breeds of dogs as to size, form, color, degree of harshness and length of coat, skull and jaw shape, length of body and of leg, temperament, vitality, and educability cover a startlingly wide range. All breeds and types of the domestic dog have come, however, from not more than two or three wild progenitors in the comparatively short space of a few thousand years. All of them from the huge St. Bernard to the tiny Mexican Chihuahua are the results of nature's variations plus man's selection.

The Horse.—The name *horse* is equivalent to the Anglo-Saxon *hors*, which means *swiftness*, and it is logical to suppose that this genus was able to survive the vicissitudes of time and enemy attack only because of its speed and mobility.

The only surviving genus of the family Equidae, to which the horse belongs, is that designated as Equus. There are at present four living types: horses, asses, half asses, and zebras. Besides the domesticated horses, *Equus caballus*, there is one wild type found in Mongolia, *E. przhevalski*. The domestic ass is called *E. asinus* and has at least two

wild varieties, *africanus* and *somaliensis*. In addition, there are three Asiatic half asses, *E. kiang*, *E. onager*, and *E. hemionus*. Among zebras, which are striped animals, there are three types, *E. zebra*, *E. burchelli*, and *E. grevyi*, and in addition several varieties of *E. quagga* (now extinct). All these species of horses, asses, and zebras are capable of producing hybrids among themselves but the hybrids are, as far as is known, generally sterile.

Equus has two close relatives among the perissodactyls (uneven number of toes), *viz.*, the tapirs and the rhinoceroses. The tapirs are rather heavy, thickset animals with stout limbs having four toes on the forefoot and three toes on the hind foot. The nose and upper lip are elongated into a flexible, mobile snout, the ears small and erect, and the tail short. The dental formula in this genus is $\frac{3}{3}, \frac{1}{1}, \frac{4}{3}, \frac{3}{3}$. The rhinoceroses are very heavy, thickset animals with very short, stout limbs and three completely developed toes on each foot. The head is large with one or two horns on the median line of the face or nose. The ears are erect, eyes small, and the skin very thick and set off into sections of indurated plates. The incisors and canines are generally lacking, giving a dental formula of $\frac{0}{0}, \frac{0}{0}, \frac{4}{3}, \frac{3}{3}$.

The members of the genus Equus are generally taller and swifter animals than their near relatives, the tapirs and rhinoceroses, their greater height being due to a lengthening of the cannon bones and middle toe. The head and tail are also longer, and the body has a much denser hairy covering. There are wide differences in the genus Equus in size, color, tail, ear, and face characteristics. The dentition of the genus is $\frac{3}{3}, \frac{1}{1}, \frac{3}{3}, \frac{3}{3}$. The horse *E. caballus* is distinguished by a long flowing mane and forelock, smaller head, broader feet, shorter ears, longer limbs, heavier tail, and also by four callosities, one on each limb on the inner surface above the "knees" of the forelimbs and below the hocks of the hind limbs. *E. przhevalski* has a short erect mane. The asses and zebras have narrow hoofs, large ears, chestnuts or callosities on the front limbs only, a short mane, and short hairs on the tail. The wild asses or half asses are intermediate with fairly long ears, a short mane, and only the front feet narrow.

Origin and Domestication of the Horse.—The horse was probably the last animal to be domesticated by man, but his immediate ancestry as well as the date of his domestication is still a matter of dispute. It seems probable that at least two or perhaps three wild types have made their contribution to our domestic horse. One of these was no doubt

the so-called "steppe horse" now known as the fossil representative of Przhevalski's horse. This was a small, sturdy, short-legged horse with a moderately long, heavy head. Another was the so-called "desert horse," standing as did the steppe horse about 13 hands high and corresponding closely to the now extinct tarpan or Mongolian horse. This strain was somewhat more slender than the steppe horse and had a shorter head. The third contribution was that of the "forest horse," a type standing about 15 hands high with longer but stout limbs and having a long, narrow head and long body. It seems probable that all three types made their contribution and that by crossing and selection

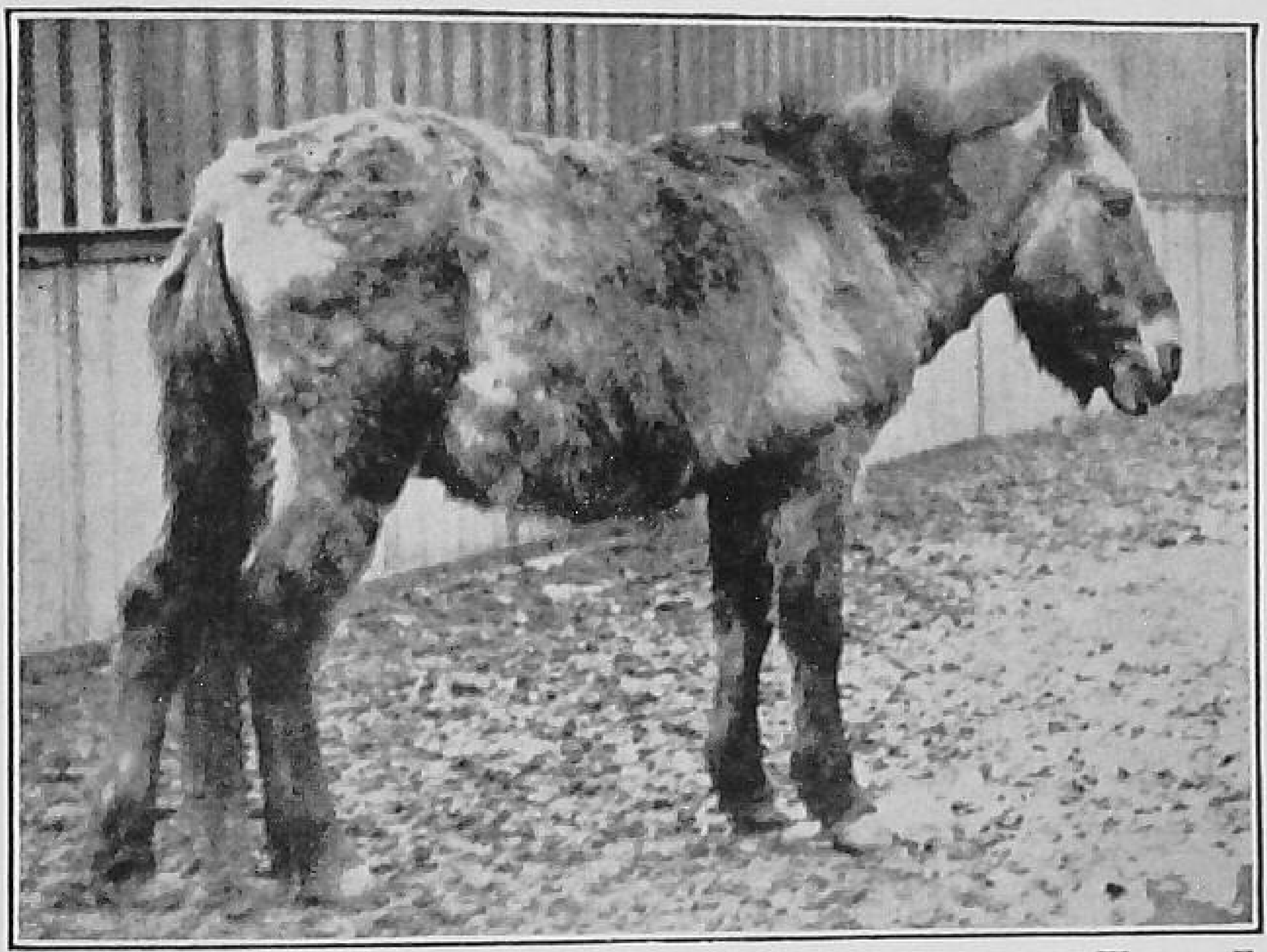


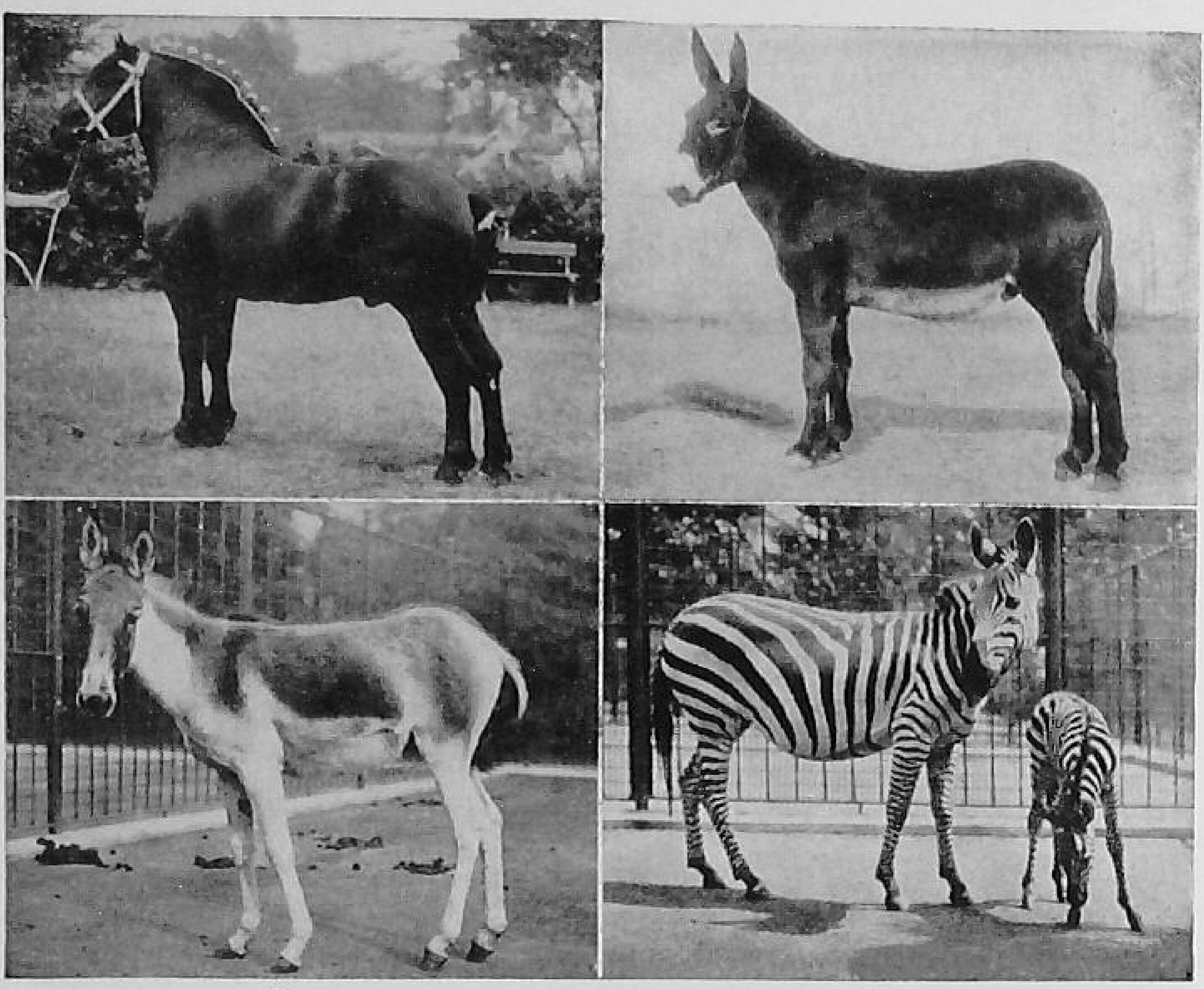
Fig. 16.—The "Tarpan," a Mongolian wild horse from which the horses of Western Europe have been derived. (*From Thompson, Outline of Science, Geo. Newnes, Ltd.*)

the foundations of our modern breeds were laid. The horse was apparently domesticated separately in both Asia and Europe, probably earlier in Asia. A Turanian folk tamed the Przhevalski horse around 3000 B.C.

The earliest record of the horse dates back to Paleolithic times about 25,000 years ago. Around an open camp at Solutré in France are found the remains of several thousand horses, indicating that they may have served as a source of food. In later Paleolithic times, rock carvings of the horse were made but do not show him harnessed, ridden, or attached to any sort of vehicle, so that we assume the horse was not yet fully domesticated.

The earliest trace of the horse hitched to a chariot goes back to about 2000 B.C. in Greece, whereas the first Egyptian records of the horse

date from about 1600 B.C. These were small horses about 13 hands high, similar to Przhevalski's horse. The horse evidently grew in size and importance in Persia and Mesopotamia during the intervening years and after about 750 B.C. began to serve as a mount. Mounted horsemen were first given a place in the Olympic games in 648 B.C. The Arabs did not use horses until after the time of Christ.



Horse Ass
Kiang Zebra

FIG. 17.—The horse and some of his relatives. (*Courtesy New York Zoological Society.*)

The development of the Arabian horse by the Bedouins of the desert is generally recognized as the first great achievement in animal breeding of which there is any definite record. Because the Bedouin's safety often hinged upon the speed and endurance of their horses, these people surrounded their breeding operations with an air of superstition and mystery, much of which has persisted in certain quarters to the present day. The Arabian breed probably was used later to refine the large "cold-blooded" horses of the countries to the west and north, particularly of France and England. The Arabs, as well as Barb and Turk horses, were also used to cross with the racehorse of England, thus laying the foundation for the Thoroughbred.

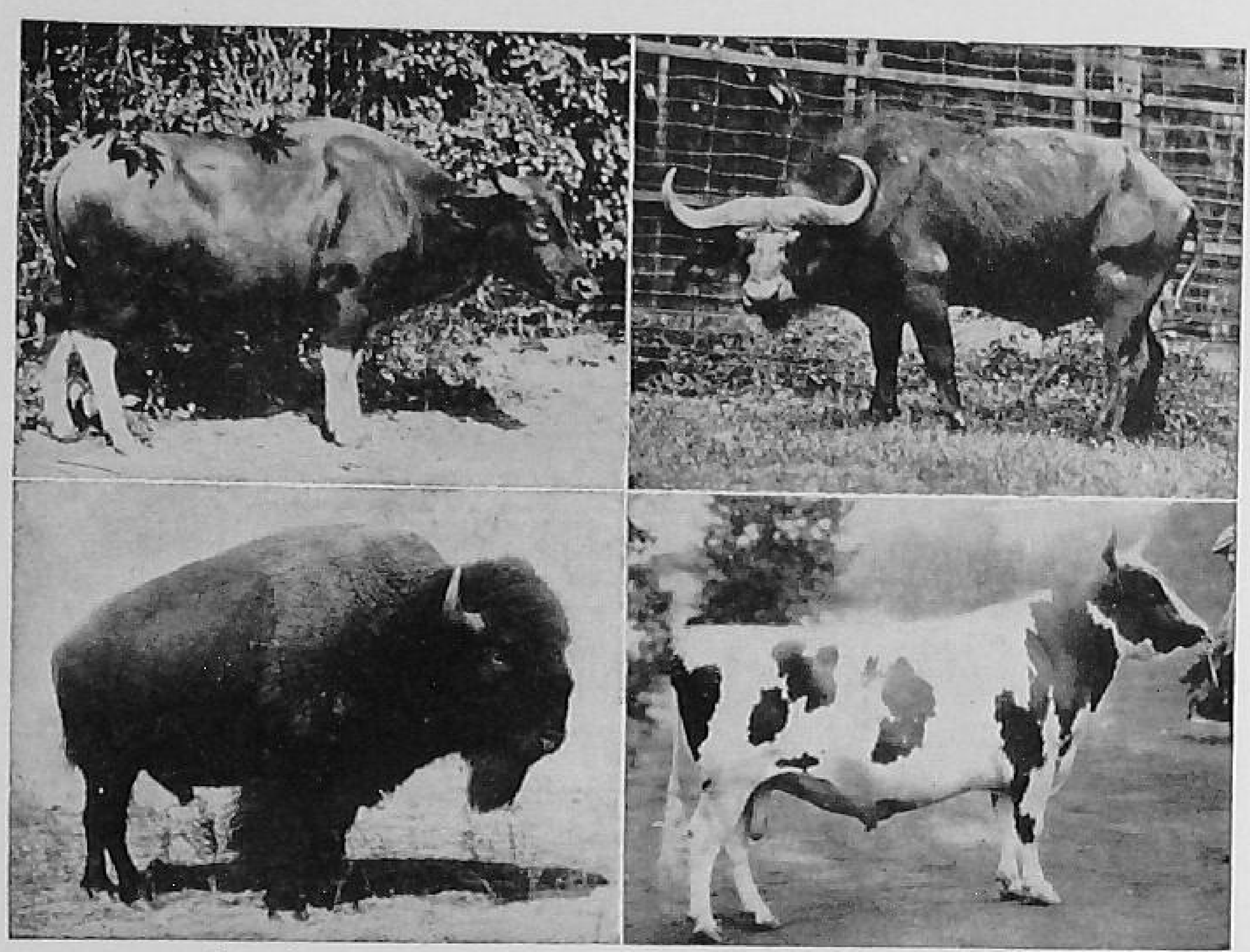
For many centuries the horse has been man's foremost helpmate in work, war, and play. He rendered incalculable assistance in conquering the New World, America. From 4,336,000 horses in 1840, the year of the first agricultural census in the United States, his numbers steadily increased to 21,500,000 in 1918. Since then he has been replaced to a considerable degree by machines, automobiles, trucks, and tractors, so that in 1950 his numbers had dwindled to about 6,000,000. This freeing of land from the production of feed for horses has complicated the situation of agriculture tremendously, and there seems now to be a definite increase in the number of horses being used for pleasure. What the future holds in regard to mechanization no one can prophesy, but it can be said with little fear of successful contradiction that our present civilization rests quite largely on the sturdy legs and broad backs of our four-footed friends and not the least among these is *E. caballus*.

Cattle.—The Pecora, or true ruminants, is made up of the following families: the Cervidae (deer), Giraffidae (giraffes), Bovidae, to which all types of cattle belong, as well as sheep, goats, and true antelopes. Both sexes in this family are usually horned. The horns are hollow and grown on bony cores and arise from the frontal bones. The second and fifth digits are rudimentary or absent, the third and fourth fully developed. The dental formula for this family is $\frac{0}{3}, \frac{0}{1}, \frac{3}{3}, \frac{3}{3}$. These animals are ungulates or hoofed and belong to the group known as artiodactyls, or even-toed. There are one or more enlargements for food storage along the esophagus, usually three, and the members of this family ruminate or chew their cuds.

The genus Bos includes the taurine group, *Bos taurus* (cattle); and *B. indicus* (humped cattle); the bibovine group, *B. gaurus* (the gaur); *B. frontalis* (the gayal); and *B. sondaicus* (the banteng); the bisontine group, *B. grunniens* (the yak); *B. bonasus* (the European bison); and *B. bison* (The American bison); the bubaline group, *B. caffer* (the African buffalo); *B. bubalis* (the Indian buffalo); *B. mindorensis* (the Mindoro buffalo); and *B. depressicornis* (the Celebes buffalo). There are many varieties under most of these species, both living and extinct. As far as known, all these species are generally interfertile and produce fertile hybrids, though the males are often sterile.

These close relatives of our modern domesticated breeds of cattle form a very interesting and widespread group of mammals. Many of them have become domesticated. Of the Bibovine group, the gaur (*B. gaurus*) is the largest of the present-day representatives and is found in India, Burma, and all the Malayan regions. It has somewhat flattened horns, a short tail, white lower extremities, or "stockings," fine silky

hair, and long spines on the anterior thoracic vertebrae forming a high set of withers, the bull standing about 16 hands high. It is a somewhat shy, forest- and hill-loving animal. The gayal is somewhat smaller with short horns and "stockinged" feet and is easily domesticated. The banteng is the smallest representative of this group, has a white disk from the hocks to the tail setting, and is somewhat longer legged. The banteng frequents the lowlands as well as the hills.



Gayal — African Cape Buffalo
American Bison — Ayrshire Bull

Fig. 18.—Some relatives in the genus Bos. *(Courtesy of New York Zoological Society.)*

The bisontine group includes the yak of Tibet as well as the European and American bison, the latter often erroneously called a buffalo. The yak inhabits the wild, cold regions of Tibet and Siberia, and it is said that travel there without his help as a pack animal would be impossible. The yak has a skirt of long hair hanging from his shoulders, flank, thighs, and tail. He is smaller than the gaur, standing about 14 hands high, and is not "stockinged" with white. The bison is characterized by very heavy forequarters and light rear quarters. His head, neck, chest, and shoulders are covered with moderately long, dark hair and like the yak he has 14 or 15 pairs of ribs. Great herds of bison once ranged over most of Europe and a goodly portion of North America.

The bubaline group, or true buffalo, includes four species at present.

The African buffalo is noted for his very heavy downcurving horns, which almost meet in the mid-line of his face, very unlike the Indian buffalo with his wide, out- and upcurving horns. The Indian buffalo is also larger, standing 15 to 16 hands high. Both the Philippine and Celebes buffaloes are much smaller in stature, and in the latter the horns grow straight back and upward from the forehead resembling the horns of an antelope. The buffalo is generally found in low, swampy regions.

Origin and Domestication of Cattle.—It seems probable that cattle were domesticated during the New Stone Age in Europe and Asia from more than one wild form. There are two types of domestic cattle now living, *B. indicus*, the humped cattle of tropical countries, and *B. taurus*, of the more temperate zones. Humped cattle were domesticated as early as 2100 B.C. Cattle play an important part in Greek mythology, were sacred animals in many older civilizations, and their slaughter was therefore forbidden. The great ox or aurochs, *B. primigenius*, which Caesar mentioned in his writings, is generally considered to be one of the progenitors of our modern-day breeds. This was a very large animal and described by Caesar as "approaching the elephant in size but presenting the figure of a bull." The wild park cattle of Britain are considered by some to be the direct descendants of *B. primigenius*. Another progenitor of our modern breeds is *B. longifrons*, a smaller type, with somewhat dished face. This is the Celtic Shorthorn which has never been found except in a state of domestication and was the only ox in the British Isles until 500, when the Anglo-Saxons came bringing with them the great ox or aurochs of Europe.

It is doubtful whether any of our present-day European or American breeds trace solely to either one of these ancient types. It seems much more probable that our present breeds are the results of various degrees of crossing between them. The cattle of India and Africa, *B. indicus*, are characterized by a lump of fleshy tissue over the withers sometimes weighing as much as 40 or 50 lb. They also have a very large dewlap and the voice is more of a grunt than a low. They are thought to be descended from the wild Malayan banteng.

It seems probable that savage man first used members of the family Bovidae as a source of food. Real domestication began when these animals were used as draft animals, probably in the first faltering steps of the beginning of agriculture or the tillage of the soil. In their wild state there was little tendency to store excess fat on the body, as this would have been a hindrance rather than a help under the conditions then existing. Milking qualities also were just sufficient for the rearing of the young. As civilization developed, feed became more abundant,

methods of caring for livestock improved, and the latent possibilities for rapid growth, fat storage, and milk production began to be realized under man's selection.

That the ox played an important part in man's aesthetic development is attested by its use in architecture and interior mural decoration as well as its frequent use as a subject of poetic fancy. The ox assumed great religious importance in many ancient civilizations, and the best members of the breed were sacrificed to propitiate the gods. They were crowned with wreaths and honored in other ways during the pageants and holidays, and to some extent we perpetuate this custom in our fairs and expositions today. The Romans used the term *pecunia* for money, a word derived from *pecus* meaning cattle, and in ancient times a man's wealth was figured in terms of his cattle possessions.

Down through the ages various members of the genus Bos have continued to be one of man's most useful allies. Without their contribution of power, meat, milk, and inspiration it is difficult to visualize the possibility of an advancing civilization. The following is G. L. Bickersteth's translation of Carducci's poem, "The Ox":

I love thee, holy ox; a soothing sense
Of power and peace thou lodgest in my heart.
How solemn, like a monument, thou art,
Watching the pastures fertile and immense!

Or 'neath the yoke with calmness how intense
Dost thou to man's quick toil thy aid impart!
He shouts and goads thee; patient of the smart,
Thine eyes, slow turning, claim more reverence.

From thy broad nostrils, black and moist, doth rise
Thy breath in fragrant incense; like a psalm
Swells on the air thy lowings' joyful strain.
Austerely sweet are thy grave emerald eyes,
And in their depths is mirrored, wide and calm,
All the divine green silence of the plain.

Sheep and Goats.—These two genera of the family Bovidae are very closely related, so closely in fact that a naturalist never speaks lightly of separating the sheep from the goats. Modern breeds are easily enough distinguishable, but the task is sometimes very difficult in their wild relatives. The genus Ovis includes the sheep and its wild relatives, whereas goats and their kind make up the genus Capra. Sheep are to be distinguished from goats by glands in both fore feet and hind feet, by the absence of a true beard, and by the absence of the strong goaty

odor in males. There are also marked differences in the skulls, and the horns generally spiral in opposite directions, the right horn of the sheep to the right like a corkscrew, and the goats to the left. The sheep gets its Latin name *Ovis* from the Sanskirt *avi*, signifying to keep or to guard.

Our domestic sheep have a great variety of wild relatives. Lydekker divides these into four groups: (1) the bighorn (*Ovis canadensis*) of North America and Kamchatka, (2) the argali (*O. poli*) of Central Asia, (3) the urial (*O. vignei*) of Asia and the mouflon (*O. musimon*) of Asia Minor and Europe, and (4) the bharal (*O. nahura*) of Little Tibet and the Barbary (*O. tragelaphus*) of North Africa.

The bighorns are a large breed of wild sheep standing 38 to 42 in. at the withers. As the name indicates, the horns are very large and are noted for the small size of the transverse ridges and the prominence of the outer anterior angle of the horn. The horns curve back, out, down, and forward in a bold sweep. The upper part of the body is covered with dark hair, the lower portion with a gray or dirty white hair. They have a very noticeable caudal disk of light-colored hair extending in a radius of about 8½ in. from the root of the short tail. They make a square track, for the interior and exterior edges of the toes are nearly parallel. The front of the toe is also beveled, which accounts for the remarkable climbing power of this group of mountain-dwelling wild sheep. The group has a very shallow lachrymal pit in the skull.

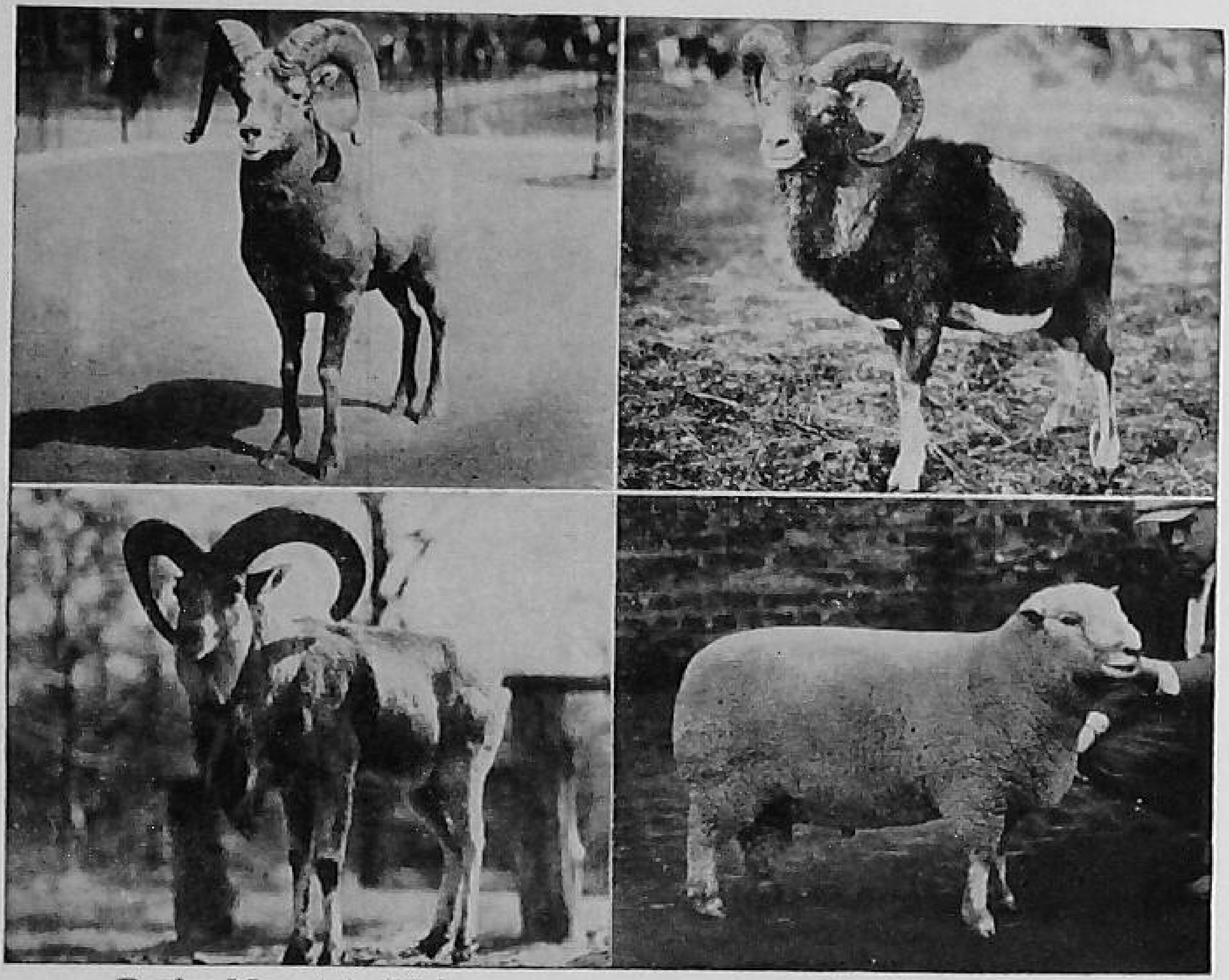
The argali, or Marco Polo's sheep, is a large species standing 40 to 48 in. high at the withers. They have strongly marked transverse ridges on the horns and a less pronounced outer anterior angle. The horns are very long (circle and a quarter) and make a wide sweep. The color of this group is very similar to that of the bighorn, including the caudal disk. These however, have a short mane on the throat. These wild sheep inhabit the grassy slopes of The Pamirs and never attain to very high altitudes. There are several closely related varieties in this group differing somewhat in size, color and shape of horns, habitat, etc.

The urials are a smaller race of sheep generally found in high altitudes. They stand about 3 ft. high and have shorter horns than the bighorns or the argalis. The general color is brownish gray with a white belly. The throat has a short beard or mane. There are several differing varieties in this group also, including the mouflon of Sardinia and Corsica. This is a small species of brownish-gray color with lighter colored underline and legs.

The bharal in many ways stands intermediate between sheep and goats. Its horns lack the deep transverse ridges of the sheep and are a dark olive-green color like the goats. It has a longer, therefore more

goatlike tail, and it lacks the lachrymal gland on the face. On the other hand, it lacks the strong odor of goats, also lacks a beard, and like the sheep has glands between the toes of all four feet. The bharal stands about 30 to 36 in. high and is a dark slaty-blue color. There is no long hair on the throat or tail. The skull characteristics of the bharal are goatlike rather than sheeplike.

The wild relatives of the goat include the ture, the pasang, generally regarded as the true progenitor of all our modern domesticated breeds



Rocky Mountain Bighorn Mouflon
Punjab Southdown

Fig. 19.—The sheep and some of its cousins. (*Courtesy of New York Zoological Society.*)

of goats, the ibex, the markhor, and the tahr. Here again we find a very wide variation in superficial characteristics among the mountain-dwelling members of the genus Capra, a detailed description of which cannot be entered into here.

Origin and Domestication of Sheep.—The sheep probably originated in Europe and the cooler regions of Asia not further back than the Pleistocene or later Pliocene. Remains of a sheep or goatlike animal have been found at the sites of the Swiss lake dwellings of Neolithic times. Sheep are thought to have been derived from the antelopelike animals allied to the gazelles because of certain similarities of the molar teeth. It seems certain that our modern breeds trace back to at least

two remote ancestors, the mouflon of Europe (*O. musimon*) and the Asiatic urial (*O. vignei*).

The sheep, most important of wool-bearing animals, was originally, as in the case of some breeds still, a hairy animal with an underfur of wool. No doubt people living in cold climates who used skins as clothing were the first to begin the selection of sheep for wool production. As in all our domesticated animals, there is wide variation among sheep. Some, like the African long-legged and Abyssinian maned sheep, bear hair instead of wool, some have spiral horns 2 ft. or more in length, others

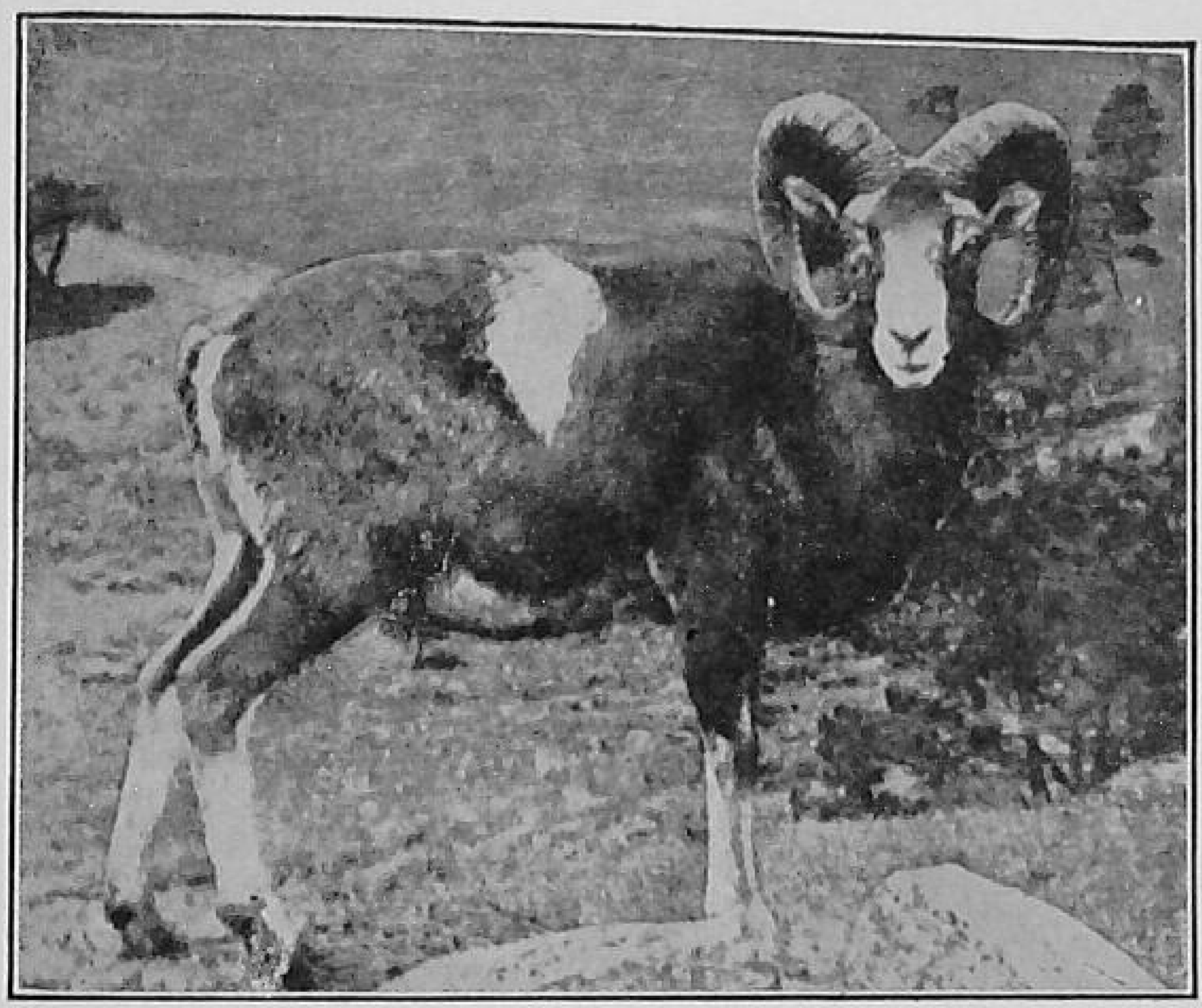


Fig. 20.—The Mouflon—a wild sheep lacking uniform color and having an exterior coat of hair. (*From Coffey, Productive Sheep Husbandry, J. B. Lippincott Company.*)

no horns at all. The tail of the common, domesticated sheep is long and slender; in some other strains, it is loaded with fat and is 1 ft. in width, whereas still others have merely a vestige of a tail. The last sort often carry huge patches of fat on the rear quarters, the stored fat in all cases serving to tide the animal over periods of food shortage. The hunia, a tall, long-legged sheep, is used in India as a fighting animal, being pitted against its fellows or other animals.

Goats are also versatile in characteristics, yielding the underfur, for Cashmere shawls, and mohair, milk, meat, and draft power and also providing one means of clearing up brush land because of their fondness for all sorts of tender shoots.

Swine.—Swine are ungulates belonging to the suborder artiodactyls (even-toed). They belong to the family Suidae. The Dicotylidae, or

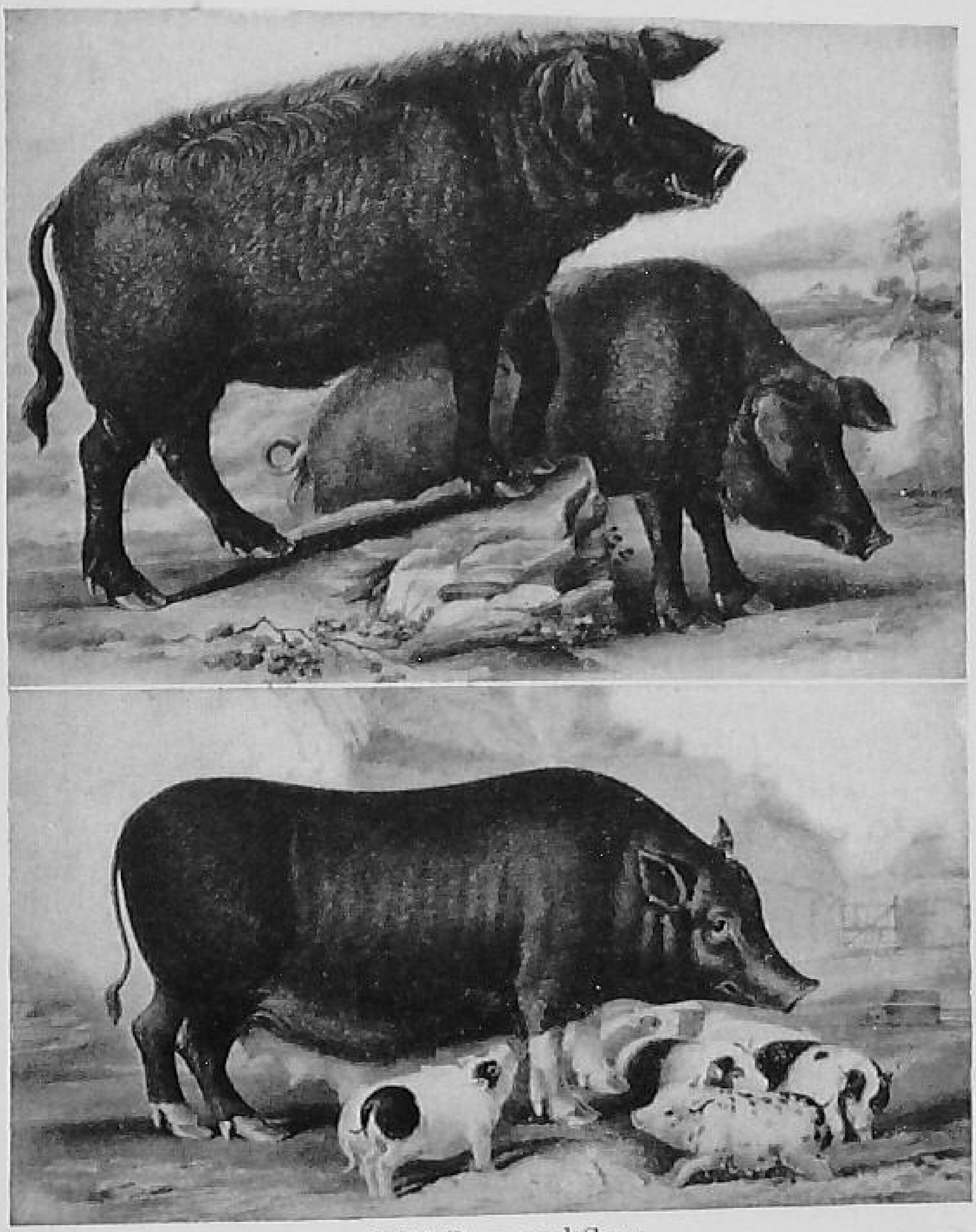
peccaries, and the Hippopotamidae, or hippopotamuses, are closely related families, these three families comprising the Suina. These animals have tubercles on the molar teeth, and in them there is not found a complete fusion of the third and fourth metapodials to form a "cannon bone." The nose is elongated into a more or less mobile snout. The typical dental formula for this group is $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$, though this is not complete in all forms.

The genus Sus includes, besides the domesticated pig, several wild species. Among them are *Sus scrofa*, the European wild boar; *S. cristatus*, the Indian wild boar; *S. andamanensis* of the Andaman Islands; *S. salvanius*, from the foot of the Himalaya; *S. vittatus*, *S. verrucosus*, and *S. barbatus* of the Malayan region; *S. africanus* and *S. procus* of Africa. The foregoing species vary greatly in size, color, length of coat, length of tail, presence or absence of crest on the neck, size of tusks, number of mammae, etc. The Indian wild boar stands 30 to 40 in. high, whereas *S. salvanius* measures only 11 in. over the shoulder. The tusks of the wild boar are several inches long, those of the red river hog, *S. africanus*, only as long as those of the domestic boar, and those of *S. salvanius* are very short. The young of all the above-mentioned species are born with longitudinal dark strips on the body which disappear as the animal matures.

Other wild relatives of the pig include the genus Babirussa of Celebes and Burma as well as the genus Phacochaerus. In the former genus the upper tusks of the male do not have their summits abraded by wearing against the sides of the lower ones as in the genus Sus, but instead the upper tusks arise close to each side of the face and pass right out through the top of the nose, never entering the mouth cavity, thence sweeping backward and upward, frequently touching the forehead, after which they curve forward, thus resembling horns rather than teeth. These tusks differ from those of the wild boar in not having a covering of enamel. They often measure 14 in. or more in length. These animals are rather "leggy" and almost devoid of hair.

The genus Phacochaerus, or wart hogs, of Africa have a head very large in proportion to the body with eyes placed far back on the face. They derive their name from the wartlike cutaneous lobes that project from each side of the face. Their upper canines are even more greatly developed than those of the Babirussa, curving upward and inward and being large disproportionately to the size of the skull. In older animals all the teeth except the four tusks and the four last molars disappear. The molars, however, measure more than 2 in. in length from front to rear, the lessened number of teeth being compensated by the over-

development of those remaining, which assures ample grinding surface. This development also occurs in the case of the adult elephant, except that in this species the lower tusks are also wanting. Wild pigs are found only in the Old World, their place in America being taken by the peccaries, a distinct family.



Wild Boar and Sow
Siamese Sow and Pigs

FIG. 21.—Probable progenitors of modern swine. *(Courtesy of Longmans, Green & Co.)*

Origin and Domestication of Swine.—It appears that our modern breeds, *S. domesticus*, have descended from at least two wild stocks; the Northern European breeds from the wild boar *S. scrofa*, and those of Southern Europe, Asia, and Africa from one of the Malayan pigs, possibly the collared pig *S. vittatus*. The former was a larger, coarser animal throughout than the latter and had a denser covering of hair.

Present-day breeds are no doubt the result of varying degrees of crossing between the parent stocks and their offspring. It seems probable

that the pig was domesticated later than cattle and sheep and previous to the horse. Selected for his ability to fatten rapidly and economically, the pig is foremost in converting feed into flesh and second to none in the economy of American meat production. Most of the breeds of hogs found in America are of our own breeders' making; *e.g.*, the Duroc-Jersey, the Poland China, and the Chester White breeds are strictly American creations.

In addition our breeders have developed the American Saddle Horse, the Standardbred Horse, the Morgan Horse, and a few breeds of sheep. For the most part, however, the American breeder's task has been simply to improve foreign breeds and to render them more suitable to our conditions.

Summary.—We have tried in this chapter to outline the events leading up to the appearance of *Homo sapiens* on this planet. He came upon the scene by slow and probably painful stages. Finally, some 10,000 to 25,000 years ago, he emerged, and his progress has been quickening ever since. We surveyed his early hunting, plant-culture, and, finally, animal-domestication phases and attempted to trace the origins of his four-footed servants. Each successive stage encouraged and made possible a larger human family. By the year 1800, man numbered 750 million. Then came the agricultural and industrial revolutions. Food became relatively plentiful, and man's procreative powers responded so well that during the next 140 years population on the earth trebled, reaching a total of over 2 billion. The world has been filling up, perhaps too fast. There are no longer frontiers, but in some parts of the world we have caught a glimpse of the abundance that should be the reward of every man of intelligence and energy. Science has now placed in our hands the tools for producing abundance. We have yet to decide what to do with them.

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Class Mammalia

Subclass I. Prototheria.
  Order I. Monotremata.
    Duckbill mole, spiny anteater, etc.
Subclass II. Metatheria.
  Order II. Marsupialia.
    Opossum, kangaroo, etc.
Subclass III. Eutheria.
  Order III. Edentata.
    Sloths.
  Order IV. Sirenia.
    Manatees.
  Order V. Cetacea.
    Whales, porpoises, etc.
  Order VI. Ungulata (hoofed mammals).
    Suborder 1. Artiodactyles (even toed).
      A. Suina.
        Families: *a.* Hippopotamidæ.
            Hippopotamuses.
          b. Dicotylidæ.
            Peccaries.
          c. Suidæ.
            True pigs.
            1. Genus Sus—Sus scrofa—wild boar.
                S. vittatus—collared Malayan pig, etc.
                S. domesticus—domestic swine.
            2. Genus Babirusa.
                Long curved upper tusks.
            3. Genus Phacochaerus.
                Wart hogs—long upper tusks.
      B. Tragulina (chevrotains).
      C. Tylopoda (camels, etc.).
      D. Pecora (true ruminants).
        Families: *a.* Cervidæ.
            Deer.
          b. Giraffidæ.
            Giraffes.
          c. Antilocapridæ.
            Prongbuck (also hollow horned).
          d. Bovidæ (Hollow horned).

Genus Ovibos—Musk Ox
↓

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      - *c.* Antilocapridæ. Prongbuck (also hollow horned).
      - *d.* Bovidæ (Hollow horned).
        - Genus Bos—Cattle
          1. Taurine group: B. taurus—ordinary cattle. B. indicus—humped cattle.
          2. Bibovine group: B. gaurus—the gaur. B. frontalis—the gayal. B. sondaicus—the banteng.
          3. Bisontine group: B. grunniens—the yak. B. bonasus—the European bison. B. bison—the American bison.
          4. Bubaline group: B. caffer—the African buffalo. B. bubalis—the Indian buffalo, etc. etc.
        - Genus Ovibos—Musk Ox
        - Genus Ovis—Sheep
          1. Bighorn group—O. canadensis, etc.
          2. Argalis group—O. poli, etc.
          3. Urial—O. vignei, etc., and Mouflon group—O. musinon, etc.
          4. Bharal—O. nahura, etc., and Barbary group—O. tragelaphus, etc.
          5. Domestic group—O. aries.
        - Genus Capra—Goats
          1. Ture group—C. caucasica, etc.
          2. Pasang group—C. ægagrus, etc.
          3. Ibex group—C. ibex, etc.
          4. Markhor group—C. salconeci.
          5. Domestic group—C. hircus.
        - Genus Hemitragus The tahr.
        - Also the various species of antelopes.
  - Suborder 2. Perissodactyles (uneven toed).
    - Families: *a.* Tapiridæ. Tapirs.
    - *b.* Rhinocerotidæ. Rhinoceroses.
    - *c.* Equidæ. Horses, asses, and zebras.
      - Genus Equus.
        1. E. caballus—the horse.
        2. E. asinus—the ass.
        3. E. kiang, etc.—half asses.
        4. E. zebra—the zebra.
- Order VII. Rodentia (rabbits, mice, etc.).
- Order VIII. Carnivora.
  - Suborder 1. Fissipedes.
    - Families: *a.* Felidæ. Cats.
    - *b.* Hyænidæ. Hyænas.
    - *c.* Proteleidæ. Earth wolf.
    - *d.* Viverridæ. Civets.
    - *e.* Ursidæ. Bears.
    - *f.* Mustelidæ. Weasels.
    - *g.* Procyonidæ. Raccoons.
    - *h.* Canidæ.
      - Genus Canis.
        1. C. familiaris—dogs.
        2. C. lupus, etc.—wolves.
        3. C. aureus, etc.—jackals.
        4. C. decussatus—foxes.
  - Suborder 2. Pinnipedes.
    - Families: *a.* Otariidæ. Eared seals.
    - *b.* Trichechidæ. Walrus.
    - *c.* Phocidæ. Seals.
- Order IX. Insectivora (moles, hedgehogs, etc.).
- Order X. Chiroptera (bats).
- Order XI. Primates.
  - Suborder 1. Lemuroidea, lemurs.
  - Suborder 2. Anthropoidea, monkeys, etc., and man.

Fig. 22.—Taxonomic arrangement of the larger farm animals.

(Facing page 66.)

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    - *C.* Tylopoda (camels, etc.).
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          1. Bighorn group—O. canadensis, etc.
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          3. Urial—O. vignei, etc., and Mouflon group—O. musinon, etc.
          4. Bharal—O. nahura, etc., and Barbary group—O. tragelaphus, etc.
          5. Domestic group—O. aries.
        - Genus Capra—Goats
          1. Ture group—C. caucasica, etc.
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CHAPTER III

ANIMAL ORIGINS AND PROGRESSION

Animals are organisms that are capable of sensation and voluntary movement. Some are one-celled, others many-celled; some move in the air, some on land, some under water; some have their supporting structures, if any, on the outside like an overcoat and are called *invertebrates;* some are supported by a bony or cartilaginous inner framework and are called *vertebrates,* species of the former far outnumbering those of the latter. Some, like man, have a very highly developed brain and sensory system for recording environmental stimuli; others, like the clam, are relatively immune to environmental changes. All must ingest food materials and oxygen and rid themselves of waste products in order to live. All are endowed with the power and "desire" to perpetuate their kind through some form of reproduction. Although they show the widest sort of diversity, there seems to be a thread of unity binding all living creatures into one organic whole. They all come into being, grow to maturity, reproduce their like, and, finally, die in very much the same fashion.

Early Ideas on the Genesis of Living Forms.—Man has been pondering the question of the whence, why, and whither of himself and all other animate nature for many thousands of years. These questions probably did not concern him in his prehuman state, any more than they concerned you and me when we were infants. With the dawn of reason and beginning of the capacity for reflective thinking, however, man began to wonder about the origin of and relationship among living forms. Until the advent of science with its inductive method of reasoning, he could but guess and speculate on these questions.

Science is nothing but the discovery and arrangement of separate facts into logical patterns of relationships or of cause and effect, the ascertaining of general laws from separate facts. Millions of facts, classified into many categories, indicate relationship between all living forms. For a full appreciation of the problems of breeding and inheritance, an understanding of the general scope of animal relationships furnishes the best medium.

Centuries ago it was obvious that the sun revolved around the earth, men saw it happen every day. It was just as obvious that the earth

was flat. In this same category of the obvious was the production of living matter from lifeless materials; maggots and flies from decaying meat, worms from manure, etc. This idea of spontaneous generation of living organisms from dead material is, therefore, of ancient origin and is probably still extant in some regions.

Most of the early Greek philosophers felt the need of offering some explanation of the genesis of living forms. Thales (seventh and sixth century B.C.) was the originator of the doctrine of abiogenesis, or the production of living forms from lifeless matter. He taught that life develops from amorphous slime under the influence of heat. Anaximander (611–547 B.C.) taught that the earth existed first in a fluid state, which later solidified in spots to form dry land, and that living creatures formed in the water came out onto the land in a gradual fashion and acquired the appendages and other bodily mechanisms which would make terrestrial life possible.

Anaxagoras (510–428 B.C.) was the first to suggest the idea that gradual development was not the result of the workings of blind force but was directed by some "Intelligence," a theory known today as *teleology*. His idea was that the germs of all animate and inanimate things existed first in chaos, but that gradually soil was laid down, covered with air, and this in turn by ether. The germs of plants floating in the air finally settled on the earth and covered the earth with vegetation. Thereupon the germs of animals and men, which he supposed were floating in the ether, settled onto the earth, grew, and prospered. All of this, according to Anaxagoras, followed an intelligent plan created by some designer; *i.e.*, the process was not inherent in the materials but needed an outside directing force.

Empedocles (500?–430? B.C.) had the notion that parts of organisms, heads, arms, legs, etc., existing first in separate states, were finally brought together into whole organisms through the triumph of love over hate, and that those which had made a lucky combination of suitably adjusted parts were able to survive and perpetuate themselves in their offspring, leaving others less fortunate in their acquisitions, to extinction. Here we meet for the first time the general idea of the survival of the fittest.

Epicurus (341–270 B.C.) and his later Roman apostle Lucretius (99–55 B.C.) taught that plants and animals arose on the earth from the action of the sun's heat on the moist earth, or, as Lucretius phrased it in his materialistic poem "On the Nature of Things," "Nothing from nothing ever yet was born." Lucretius anticipated Dalton and modern chemistry in his reference to the atomic nature of matter as well as Mendel and modern genetics in his reference to hereditary bodies within the mother.

Aristotle (384–322 B.C.), one of the most renowned of the Greek philosophers, believed, as did Anaxagoras before him, that some intelligence, entelechy, or "soul of living things" directed the process of the active generation of living forms from passive matter. This soul property was thought to be present in increasing degrees in earth, water, air, and fire, so that the earth produced plants, water produced aquatic animals, air gave rise to terrestrial organisms, and fire the supposed inhabitants of celestial bodies. Aristotle maintained that plants and many animals, *e.g.*, worms, insects, crabs, and other marine forms and even man, might arise spontaneously, all the former from the dew, slime, manure, sweat, meat, decaying trees and fruit or seawood, or from the moist earth, whereas man's first appearance was thought to have been in the form of a worm. Aristotle's teachings dominated men's thinking down to the time of science, and the acceptance of his ideas by St. Augustine (A.D. 354–430) established spontaneous generation as a dogma of the Church. St. Augustine and others of the early Church fathers, however, were not literalists in regard to the Mosaic account of creation but interpreted the 6 days of creation to be periods of time much in excess of 24 hours.

Aristotle's works were translated by the Arabs in the ninth century and found their way into Spain a century later. The revival of these pagan Greek ideas caused considerable friction in the Western European Christian world of the twelfth and thirteenth centuries, but a synthesis of Greek scientific and Christian theological ideas was finally achieved by the great churchman St. Thomas Aquinas (1215–1274).

Unlike Aristotle, who wanted to understand and eventually control nature for beneficial human ends, the churchmen of the Middle Ages started with some acceptable belief. Their ideal was the contemplation of truth arrived at through intuition and faith. They believed that they knew the purpose and meaning of existence and that the function of nature and of man was to glorify God. The Scholasticism of St. Thomas was a synthesis of Greek reason and Christian faith on the theory that reason and faith are not antithetical but supplementary, and that faith can go beyond reason and solve problems for which reason is inadequate. Intuition was thus judged to be superior to reason, and for 600 years this idea, together with the authoritarianism founded on Aristotle's works, prevented scientific inquiry into the nature of the universe and man. All inquiry into the nature of things thus became heresy, and for nearly 600 years anyone who deviated from this pattern was forced to recant.

But the flame of curiosity was not entirely extinguished, and the noted Italian Leonardo da Vinci of the fifteenth century, scientist as well as painter, pioneered in the field of paleontology, one of the pillars on which

the theory of the gradual diversification of living forms now rests. In the sixteenth century, Giordano Bruno (1548–1600) espoused the Greek idea of gradual development and left among other maxims, "The investigation of Nature in the unbiased light of reason is our only guide to truth." He was finally burned at the stake for his refusal to recant his heretical beliefs.

From the liberal ideas of the early Church fathers, the pendulum swung, by the middle of the sixteenth century, clear over to the extreme literal position. Separate creation and the general over-all authority of the Bible both as spiritual guide and scientific textbook were firmly entrenched, and all doubters or too persistent seekers of nature's truths by means of reason or experiment were labeled heretics and forced to recant or be liquidated.

In the last half of the sixteenth century, and still more in the seventeenth century, curiosity and experimentation began to make some headway, but spontaneous generation held its place in the minds of men like Harvey (1578–1657), Descartes (1596–1650), Newton (1643–1727), Buffon (1707–1788), and even Lamarck (1744–1829).

Redi (1626–1697) was the first to show that decaying meat or fish could not produce maggots if flies were prevented from laying their eggs thereon. Leeuwenhoek (1632–1723), the Dutch naturalist, revealed, through his invention of the microscope, a whole new world of tiny living forms, which tended to strengthen the belief in spontaneous generation although he himself considered the forms of organisms infesting rotting meat, etc., to be air-borne. Spallanzani (1729–1799), the Italian scientist, Schwann (1810–1881), the German anatomist, and many others devised experiments to try to disprove spontaneous generation in materials uncontaminated by organisms and were generally, though not always, successful. It remained for Louis Pasteur (1822–1895), the great French chemist, to provide, by means of his bent-necked flasks, the final obituary to this age-old idea of spontaneous generation of living organisms.

There are three possible ways for accounting for life on the planet Earth. Spontaneous generation in its ancient sense seems to have been finally ruled out. To think that life was wafted to this planet from some other heavenly body only moves the problem back one step where it is entirely insoluble, and modern astronomical conceptions lend no support to the plausibility of the idea. Still a third possibility is to say that life has existed and will exist eternally. This again is impossible of proof and not very satisfactory to a practical mind.

Modern Ideas of the Beginning of Life.—From Pasteur's work came the final proof that fully formed living organisms cannot be formed in an instant and *de novo* in any sort of a culture. By some this was interpreted

to mean that there could never be or have been a transition from nonliving to living material. We know, however, that dead bodies of animals and plants are finally broken down into inorganic compounds or into the elements. The question is whether the reverse process could ever have taken place. It is now coming to be generally agreed that it not only could but did so happen, not that we now have final proof or that the biochemist can now make life.

The most probable general steps in the process seem to be about as follows: (1) the pulling out of material from our sun by the near passage of another star some 1 or 2 billion years ago and the centralization of this material to form our planetary system, including the earth with its central molten metal core covered by a layer of igneous rocks and enveloped in an atmosphere of aqueous vapor; (2) formation of hydrocarbons by the interaction of carbides of iron and other metals and water; (3) formation of ammonia by the interaction of metal nitrides and water; (4) production of numerous high-molecular compounds through condensation, polymerization, and oxidation-reduction reactions of the derivatives (alcohols, aldehydes, ketones, organic acids, etc.) of the primitive hydrocarbons and nitrogen-bearing compounds to form simple compounds of a protein nature; (5) formation of a primary colloidal system; (6) natural selection of those colloidal systems with a highly developed physicochemical organization surrounded by a semipermeable membrane capable of reproducing themselves and also capable of continued growth and variation.

This is admittedly a very sketchy picture. Detailed knowledge of the internal structure of the simplest living forms is not now available. Nature has been made to yield many of her secrets, and it seems not improbable that the true nature of living matter will sometime be discovered. Granted the formation of even the simplest living and reproducing forms together with the principle of variation, an orderly progression of living forms from the simplest to the most complex becomes thinkable.

One-celled to Simpler Living Forms.—Students as well as laymen are sometimes prone to look upon single-celled organisms as the smallest and simplest manifestation of life, but this is an erroneous view. The single-celled plant or animal is actually very complex and endowed with the capabilities of nourishing itself, of getting rid of its waste products, and of reproducing. The planet Earth is thought to have existed for about 2 billion years, and it seems probable that, after life arose from inorganic materials, it took several hundred million years to work up to the level of single-celled plants or animals.

Let us then start with single-celled forms but reverse the usual process and try to work back to the original form of life, though we should be

wary and not expect to get a necessarily definite answer at the present. The single-celled organism, *e.g.*, amoeba, yeast, etc., as already indicated, is a complex structure and is organized in a definite way. It consists of a cell wall surrounding cytoplasm in which are located chloroplasts, chromoplasts, leucoplasts, chrondriosomes, centrosome, fat droplets, mineral deposits, yolk granules, and a nucleus, the latter often containing dark-staining bodies called *chromosomes.* It has now been established that the chromosomes are the bearers of hereditary potentialities in the higher plants and animals and, therefore, form the bridge of inheritance between succeeding generations. The chromosomes are aggregates of genes arranged in linear series, whereas the genes themselves are probably complex organic molecules.

As we start down the scale in size, we come first to the bacteria. There are many thousands of these forms and in general they are rodlike, round, or spiral-shaped. We are inclined to think of them as enemies to man as those which cause typhoid, pneumonia, and other diseases surely are, but there are thousands of them that are harmless to man and many more which are definitely beneficial, *e.g.*, those soil bacteria which fix nitrogen from the air, those which convert alcohol to acetic acid, or milk curd to cheese.

Ordinary bacteria range in size from about 500 to 750 mμ. Even the highest powers of the microscope cannot at present disclose much concerning their internal structure, although we have a right to believe that they do have a very definite and specific structure. They produce variations that are definitely heritable, and, although we are unable to see a nucleus and its chromosomes within them, it seems a fair assumption that they do actually have some such mechanisms. Stoughton (1929) and Barnard (1930) have shown that at the time of fission the scattered chromidia of certain bacteria aggregate into an ill-defined mass within the organism, which then divides to produce two cells. Here apparently the genetic or hereditary materials are scattered, whereas in the one-called organisms, discussed above, they have become definitely and permanently organized into chromosomes.

It is known that living entities of a diameter below 300 or 400 mμ exist, although they cannot be seen even with the most powerful microscope we now have. These materials are called *filtrable viruses* or *filter passers* and are the cause of certain diseases such as smallpox, yellow fever, rabies in man, and foot and mouth disease in cattle and swine; but, as with the bacteria, there may also be beneficial ones. Some of them have been photographed in recent years by means of the shorter wave ultraviolet light and more recently with the electron microscope. Although they cannot be seen, they undoubtedly are living materials, for

they can produce their like on suitable culture media. In size the viruses are thought to scale down to about 10 mμ.

In the same range of size are also found the bacteriophages, or bacterium eaters. These agents live on young cultures of bacteria which they cause to disintegrate or dissolve. As the amount of bacteria decreases, the amount of phage increases. As the viruses can live only on living culture tissue so can the various phages live only on suitable bacteria. The phages are thought to be much smaller than most viruses, probably from 25 to 60 mμ. Because both the viruses and the phages have very specific properties and reactions with their respective hosts, it seems logical to infer that they have definite organization and the ability to transmit their characteristics to their offspring perhaps by means of genes. The fact that the known phages and viruses depend upon other organic forms higher in the scale of life as sources of food material may be advanced as an argument against their having preceded the higher forms in time. It is a valid objection. Two escapes from the dilemma are possible: (1) that earlier forms of phages and viruses were not so limited but endowed with the power of subsisting on simpler organisms, compounds, or directly on inorganic materials and (2) that the present parasitic forms of phages and viruses are simply examples of these general classes of organisms which have changed from earlier habits into that of being parasitic on higher forms.

Recently an American biochemist, W. M. Stanley, succeeded in crystallizing the virus of tobacco-mosaic disease. Other viruses have since been secured in a crystalline or partially crystalline form. Various nonliving materials like cane sugar as well as complex proteins and enzymes also have the property of forming crystals. Protein molecules scale down to around 4 mμ, whereas starch and sugar molecules are thought to be of about 2 and 1 mμ, respectively. From this point, we proceed down to individual atoms of unknown size and finally reach what is considered to be the basis of all matter in the universe, protons, electrons, and neutrons.

The best guess at the moment seems to indicate that under suitable conditions various elements and compounds on the surface of the earth or in the warm seas became organized into very simple forms of living material with the power of nourishing and reproducing themselves. Very likely this process occurred in a variety of places, and, for all we know to the contrary, this form of spontaneous generation may still be going on. The materials so formed were probably relatively stable, but with a tendency for polymerization as well as for various rearrangements of their atoms and molecules to produce somewhat different forms. From

these earliest living forms, there perhaps eventually came to be organizations of materials resembling the gene.

Existing singly at first, the genes perhaps gradually combined and took on a protective covering resembling at this point chromosomes. Later, cytoplasmic materials and a cell wall may have been added, and after a few hundred million years development may have reached the one-celled amoebalike stage. Growth, aggregation, variation and differentiation, and specialization of function proceeded, yielding finally the hundreds of thousands of plants and animals that at present inhabit the earth. It hardly seems necessary to say that we need not expect to find traces of the earliest forms of life, because they were too small for us to see and also because of their fragile nature. The developmental process, then, may perhaps logically be thought of as progressing from the elements to organic substances, to genes, to chromosomes, to single-celled, and finally to multiple-celled organisms and plants.

One-celled to More Complex Living Forms.—It is beyond the scope of this chapter to do more than point out the general road that progressive development apparently has traveled. The first step was perhaps the formation of various hydrocarbons. Next may have come the conversion of the above-formed carbohydrates into an amino acid by the addition of nitrogen and the conversion of the amino acids into a protein through fusion of many amino-acid molecules into one finally complex molecule. Somewhere these minute and relatively simple molecular aggregates must have become endowed with "life," especially in the sense of being able to reproduce themselves as the genes apparently do today.

The reverse of the process described in the previous section might lead from this genelike structure to a microscopically visible one-celled organism after the passage of hundreds of thousands of years. From this one-celled stage we pass to a colony of cells such as the Gonium, or free-swimming colony of 16 cells, or Volvox, in which the cells are arranged in a hollow sphere with (1) division of labor and (2) differentiation into soma and germ cells. The next step is the invagination of one side of the hollow-sphere stage forming a hollow sack two cells deep with the outer cells specialized for locomotion, sensation, and protection and the inner ones for digestion. Here the same opening serves as mouth and vent. Next we find the opening continuing through the body with a separate mouth and vent. Segmentation has taken place, the worm being an example of this stage.

Now we pass to the forerunner of the vertebrates with well-developed gill clefts and an outpouching of the gut region which will one day produce the notochord and eventually the backbone of higher types. The

cartilaginous ring at the mouth of the fishes gives us our first indication of jaws, although the vertebrate jaw develops from the first set of gill bars. We also find here our first true division into two sexes, which will persist right up through the higher animals, including man. Here we should mention too the Dipnoi, or lungfishes, which are intermediate between the fish type and amphibian, though they have only a two-chambered heart. The first land-living forms are believed to have come from the lobe-finned ganoids, which like the Dipnoi had an incipient lung.

Amphibians such as frogs and salamanders now appear. They spend their early life in water and later life on land. They have a three-chambered heart and, in place of fins, five-fingered limbs connected to the body by pectoral and pelvic girdles. After them come the reptiles, some gigantic in size though so well adapted to their environment that they could not change when it did and so became extinct. Here the gill clefts are still retained in the embryo but the young have lost gills, and the eggs are laid on land rather than in the water. In the higher forms, traces of the fourth heart chamber appears.

From this reptilian type were developed both bird and mammalian forms. Archaeopteryx was a primitive bird type in which the teeth were still retained and the three fingers of the forelimbs were still distinct and used for climbing. In modern birds the teeth have been lost, and the fingers are united by a web. At the summit of the tree of life comes the Mammalia, to which class man himself belongs.

The lowest mammalian forms are those like the spiny anteater and duckbill mole. In these forms the egg is still laid outside the body and the digestive tract and urogenital organs empty into a cloaca as in reptiles and birds. Hair has now replaced scales, and a diaphragm separates the abdominal from the thoracic cavity. The brain is not deeply wrinkled as yet, and the nutritive glands are scattered over the belly region of the female and give out a fluid that is licked up by the young.

The second stage in the mammalian group is represented by the marsupials, such as the kangaroos and opossums. The young are born immature and are placed in a pouch on the mother's belly where they complete their embryonic growth. These species are viviparous and have separate openings for urogenital and alimentary tracts as well as a distinctly four-chambered heart.

The highest stage that the process has yet reached is that of the placental mammals. In these the embryo is retained for a longer time in the mother's womb and connected to the mother for nourishment at the placenta. Here the brain is more convoluted or creased. The mammae, or teats, are well-developed for suckling and arranged over the belly region usually in two rows, although in the highest types they

become restricted to the breast region. Representative types here are the ungulates or hoofed animals such as horses, cattle, sheep, swine, etc., the carnivores such as cats, dogs, wolves, tigers, etc., rodents such as rats, squirrels, etc., anthropoids such as apes, gibbons, gorillas, orangs, chimpanzees, and, finally, man himself.

In the anthropoids we find a continued shortening of the snout region and the gradual assumption of an upright position, first evidenced through the use of the arms in swinging in the trees. The increasing size of the brain further shortened the snout, caused the further arching upward of the skull, and eventually threw the face into a similar plane to that of the vertebral column. The gorilla spends most of his time in the trees, although he does walk clumsily on his hind legs, but his long arms touch the ground frequently—a necessity if he is to keep his balance. The gibbon, a more primitive form than the gorilla, also walks on the hind legs and uses the arms for balance.

The upright position largely frees the front legs from supporting the body and enables the hand to develop as a grasping organ, to pick up and examine food, and to bring it to the mouth, which is now so greatly flattened that it is not so well-suited for picking up food as in long-snouted animals. This also frees the hand for development as a tool-using member, and even the higher apes are able to learn to use simple implements wielded by the hand. The baboons frequently use sticks to pry up stones in search of food. Chimpanzees use stones to crack nuts and sticks to pry things they cannot move with their fingers.

Organic Evolution.—The process sketched in the preceding section is generally known as *organic evolution*. By definition it is "the theory that the various types of plants and animals have arisen by descent with modification from other pre-existing types." Because man is apparently one of the latest products of the evolutionary process, our evidence for it is indirect. From the researches of physicists, chemists, paleontologists, and biologists, we can assume that matter in our solar system has progressed through a succession of stages from electronic to atomic to molecular to colloidal-organic to living forms. The most interesting phase of the process from our standpoint is the development of mind. This arose gradually and has reached its highest present level in man. It has provided the means for increasing control over and independence from the environment and at last enabled us to catch a glimpse of the processes of the universe. Contrary to some opinion, as our knowledge broadens, our reverence deepens.

This view is diametrically opposed to the supernatural theory of separate creation of each species or breed. We cannot here go into the philosophical implications involved in these two contrasting theories.

Each individual should think out his own philosophy of life rather than accept someone else's. There are two doors leading into the office where the writer is now working, and, although from a scientific standpoint, it might be important to determine which door one used for entrance, after all, it is not a very important moral or ethical question whether one entered by one door or the other. That one arrives at his destination is certainly of greater ethical importance than his method of travel. The mystery, as well as the beauty, of life is here with us now and we are part of it. How these qualities and we ourselves arrived, we do not exactly know, and perhaps we never shall. The question as to who made the universe and why may finally prove to be rather overlarge for our human faculties, but this need not necessarily plunge us into a state of cynicism, boredom, peevishness, or hostility. We are not here concerned with the question as to "why" life is now found on this planet; nor are we primarily concerned with its mode of origin or its ultimate end. The first and the last of these questions rightfully belong to the field of philosophy.

Science, which is but another name for organized knowledge, is concerned with the mode of origin of living things, but as yet it has no definite answer to this problem. The theory of evolution accepts life as a fact and tries to trace its course through the ages. Once given a living entity that is not immutable but rather prone to vary, the task of the biologist is to ascertain the causes of variation and finally to shape and to mold them to more desirable human ends.

The concept of an evolutionary process is not new, for in its broad outlines it was sensed by early Hindu and Greek philosophers. They merely had the vague notion but were able to adduce no proof. The early fathers of the Christian church seem to have been rather liberal-minded men, but the dogma of the special creation of species and the literal interpretation of the Mosaic account of creation soon came to be the accepted belief. During the difficult Middle Ages, little or no thought could be devoted to questions of this nature. There are occasional references to the general subject in the later writings of men like Bruno, Francis Bacon, Leibnitz, Linnaeus, and Kant, although most of the men of these times who thought about the matter at all believed in the separate creation and the immutability of species.

Buffon (1707–1788), a French naturalist, greatly enlarged the concept of mutability through direct environmental means, an idea which he developed in later life after having earlier subscribed to the idea of immutability. He is a precursor of Lamarck and perhaps also of Darwin in regard to pangenesis as well as the struggle for existence and the survival of the fittest. Coupled with his idea of change due to environmental influences was his further implied belief that these so-called

"acquired" characters were heritable. Buffon's chief part seems to have been that of suggesting broad new vistas, rather than filling in details, asking questions for his followers to answer, or opening up new fields for conjecture and experimentation. To him goes the credit for beginning the consideration of organic development from the observational and inductive standpoint.

Erasmus Darwin (1731–1802), an English physician and poet and a grandfather of Charles Darwin, is one of the most imposing figures in this field of human inquiry. He borrowed and enlarged on many old ideas concerning evolution and made distinctive new contributions of his own. He was the first to stress the idea that evolution has been operating from the time of the first primordial life. To him new forms were but the flowering of potentialities originally deposited in the life stream by the Creator and called into being by the necessity for adaptation. He foreshadows the work of his grandson Charles in allusions to man as an offspring of lower quadrupedal ancestors, in some of which the thumb had accidentally come to lie opposed to the fingers, giving a hand that led finally to the great development of the human mind. He assumed a simple living filament endowed with irritability and sensitivity as the progenitor of all that lives. The first living material was endowed with potentialities for new developments that were called out by the organism's response to pleasure and pain. He followed Buffon and anticipated Lamarck in his belief in the inheritance of acquired characteristics.

Lamarck (1744–1829), a French botanist and zoologist, can be rightfully called the father of the modern theory of evolution owing to his having been the first to devise a phyletic tree to include all plants and animals. He was the first to state that all animals formed a branching series of related forms, shading into each other but with many gaps due to the intermediate forms not yet having been discovered. He believed that small masses of mucilaginous matter took on living properties and became elemental plants or animals. His theory of evolution propounded in 1809 has three main points: (1) that the environment, directly in plants but indirectly in animals through the medium of the nervous system, calls out changes in the organism, (2) that the use or disuse of parts leads, respectively, to their further development or to their atrophy, and (3) that these so-called "acquired" characteristics are inherited.

The main idea to be noticed here is Lamarck's belief that the environment is the principal cause of change. This is similar in its general outline to Buffon's earlier belief that something external to the organism brings about changes rather than something within the organism. Geoffrey St. Hilaire (1772–1844), another French zoologist, subscribed to Lamarck's idea that the environment caused the developmental

process but by means of changes brought about in the embryonic or germinal condition rather than in the adult. He thus, in a sense, anticipated Weismann's idea of germinal variation and causation as well as De Vries's idea of evolution by means of large jumps or mutations, for his work in the field of teratology made him acquainted with sudden departures from type that, he reasoned, might give rise to new species.

Goethe (1749–1832), the great German poet and philosopher, was, in his earlier days, a scientist working in the fields of botany and anatomy, contributing original papers on the metamorphoses of plants and suggesting, erroneously, that the skull was of vertebral origin. He vigorously opposed the idea of the fixity of species and upheld that of descent with modification, or of the ascent of man from some lower form. In the decade between 1780 and 1790, Goethe provided the beginnings of one of the pillars on which the theory of evolution rests, *viz.*, that of comparative anatomy and embryology. Osborne yields him the honor of being the first man to conceive evolution in the modern sense and says that the transfer of his affections and abilities to the field of literature retarded the demonstration of the law of evolution by half a century. He first offered the correct solution to the riddle of vestigial structures as remnants of those which were necessary further down the scale of life and foreshadowed the dual nature of the process—its centripetal, conservative, hereditary force and its centrifugal, progressive, variational force.

Cuvier (1769–1832) was a champion of the fixation of species and a stout opponent of transformism. He, nevertheless, was the founder of paleontology, which furnishes still another of evolution's supporting pillars. He explained the series of different forms in the earth's crust as due to catastrophic extinctions and later migrations, whereas some of his students and followers said they were each due to a separate creation. Cuvier's exalted place in the science of his day served to retard the acceptance of the idea of mutability, and his brilliant pupil Louis Agassiz was never convinced of the reality of transformism.

Several noted embryologists of the early nineteenth century stressed the mutability of species and called particular attention to the many similarities between different animals in their early embryonic states and to the fact that the higher animals pass through stages which form the terminal point for lower animals. Many other writers in the first half of the nineteenth century had inklings or convictions about "creation by evolution"; and two of them, Wells in 1813 and Matthew in 1831, recognized the principle of natural selection, which was to form the cornerstone of Charles Darwin's theory as expressed in "The Origin of Species."

Opposition to Mutability.—We should here remind ourselves that in

this brief review of the history of men's thinking about animal origins up to the time of Darwin, we have said nothing of the general opposition to the theory of gradual change. True there had been martyrs to this general idea back in the fifteenth and sixteenth centuries, and many others had been forced to recant. The general populace, however, knew little or nothing about such things. Life here was hard for the mass of mankind, but they had what seemed a sure promise of a better one to come. The Roman Church and its Protestant derivatives alike frowned upon any views of man's relation to the universe other than those given in the Mosaic account. So although the general idea of change had had a long history and its development had been contributed to by scores of men for over 3,000 years, yet mankind as a whole was both ignorant of what had transpired and bound by certain dogmas directly antithetical to the idea of evolution. But into this hostile, prejudiced atmosphere the idea did finally come in 1859. It has had a stormy passage but is now accepted by most educated people, for it seems to offer the best available solution to the age-old problem of the whence of animal forms.

Darwinism.—Charles Darwin (1809–1882), to whom reference has already been made, was an English naturalist. He had been educated in the universities of Edinburgh and Cambridge, studying both medicine and theology. He practiced in neither field, however, and wrote later, "My scientific tastes seem to have been certainly innate . . . I consider that all I have learnt of any value has been self-taught." The foregoing pages will have indicated that Darwin was not the father of the idea of gradual progressive change. He might perhaps more correctly be called the *attending physician* who brought the conception safely into the world, or as Butler said, "Darwin's chief glory is not that he discovered evolution but that he made men believe in it, and what glory," he added, "could be greater than this?"

Darwin sailed on H.M.S. *Beagle* as naturalist on a round-the-world trip lasting from 1831 to 1836. On this voyage he had the opportunity of studying the rich fauna and flora of South America and several island archipelagoes and was struck by the manner in which animal types shade into each other as well as by the distinctive forms found on separate islands. He began this journey with a belief in separate creation, but the facts he observed caused him gradually to give up this explanation for that of the mutability of species. On his return to England in 1837, he began to collect facts on plant and animal variation and during the next year, while reading Malthus's "Essay on Population," the idea of the struggle for existence that is constantly going on in nature as an explanation of the great variety of plant and animal species came to him as it had previously come to Wells, Matthew, and perhaps many others.

Darwin's thesis involved four points: (1) that organisms vary, *i.e.*, are not exactly like their parents, which no one can successfully deny; (2) that these variations are or may be hereditary, *i.e.*, passed along to future descendants, which again is a commonplace; (3) that there is a continual struggle for existence in nature; and (4) that those best fitted to survive in the given environment will be the most apt to survive and should, therefore, leave the most descendants, which seems to be a very logical assumption. He thought that the working of the above-named four principles would account for the great variety of forms of plants and animals which now inhabit the earth or have inhabited it in the past.

Darwin accepted evolution as a working hypothesis, accepted the obvious facts of variation and hereditary transmission of potentialities, and adduced a tremendous amount of data that seemed to support his thesis that natural selection or, to use Spencer's term, "the survival of the fittest," is the leading actor in this drama of survival. Darwinism is not the process of gradual development itself but is one suggestion as to how evolution works. Discussions among biologists, therefore, regarding the correctness or incorrectness of Darwinism are discussions regarding the mechanism of evolution, not questionings of the process itself, which practically all biologists and other scientists accept as a very probable—as the most probable—fact.

Darwin saw that organisms vary. He had observed the keen competition to survive in both the plant and animal world, and, when these two ideas are added, the sum is inevitably natural selection. As has been said, the title of Darwin's book should have been the "Survival" rather than the "'Origin' of Species." He accepted variation as he saw it without attempting to explain its underlying causes. He accepted the older ideas of the influences of use and disuse of parts in causing development or atrophy. He concurred in the belief that the environment could cause heritable variations. He made no distinction between germinal and environmental variations. He believed to a certain extent at least in the inheritance of acquired characters and formulated a mechanism for its operation in his theory of pangenesis, *i.e.*, gemmules from all parts of the organism being deposited or registered in the germ cells ready to be passed along to the next generation.

It would have been truly miraculous if Darwin had made no mistakes. Little was known at the time about germ cells and their cytology. Chromosomes, now the accepted bearers of hereditary potentialities, were undreamed of, and naturally the synthesis of cytology and genetics into a firm foundation for biological thought was lacking.

Darwin did not distinguish between genetic and environmental variations but depended on a "strong principle of inheritance" that pre-

sumably included both. Later research has shown that the germ cells, ova and spermatozoa, are the bridge of inheritance between parents and their offspring, and numerous attempts to demonstrate the inheritance of acquired characteristics (environmental variations) have failed. Darwin accepted all variations as potentially heritable and was concerned with the mechanism that allowed some variants to survive and breed successfully, whereas others failed. His conclusion was that the environment acted as the selecting agency, preserving some variations while

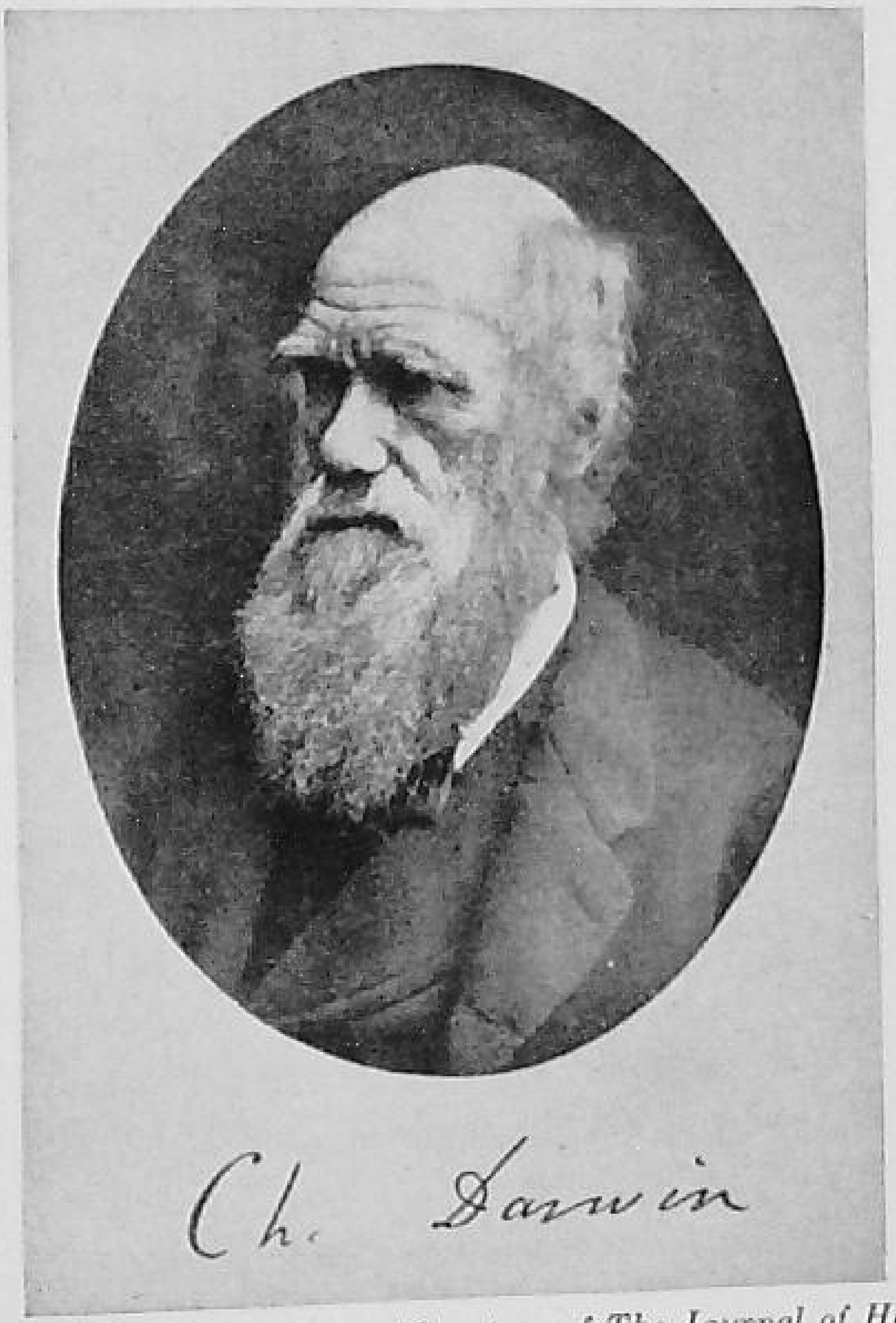

Fig. 23.—Charles Darwin. (*Courtesy of The Journal of Heredity.*)

destroying others. This is known as *natural selection*. He built his theory on the cumulative action of a multitude of small variations and looked with disfavor on the possible contribution of big jumps, saltations, or mutations.

Darwin's success was due to his care and patience in gathering facts, a task to which he devoted 25 years, and to his formulation of a workable theory into which the facts would fit. He used the inductive method of science, from facts to general principles rather than the deductive method of principles to facts. He believed that variations occur at random and asked Heaven to "forfend him from Lamarck's nonsense of a tendency

to progression or from the slow willing of animals"; in other words, he did not believe in some outside design.

A. R. Wallace, another English naturalist and contemporary of Darwin, reached a conclusion very similar to Darwin's at about the same time, although he had not marshaled so much data to support his thesis as had Darwin and therefore like a true gentleman and scientist yielded first place in this field to Darwin.

Natural Selection.—Thus far no better theory for the appearance of new species has been suggested than Darwin's natural selection among naturally arising variations. Darwin did not try to account for the origin of new heritable variants that might in time become new species. Concern over natural selection, adaptation, and the building of hypothetical classifications probably did much to retard inquiry into the basic facts regarding the origin and mechanism of hereditary variations and their mode of transmission. It was not until the twentieth century, through the synthesis of chemical, physical, genetic, and cytological sciences, that we were to begin to have a clear conception of the basis of living matter and its gradual development through germinal changes.

There have been many attempts to deny the validity of the cornerstone of Darwin's theory, natural selection, and likewise many attempts to replace it with other theories. These in general take two forms: one the substitution of orthogenesis, or progression from natural causes in a straight line, for Darwin's random variation; and the other an appeal to an internal, mystic directing force within the living material.

For the emergence of complex from simple animal forms two things are necessary: (1) living material and (2) some variation. These are obvious to any observing person, and there has yet to be suggested a better selective agency than the one proposed by Darwin. In many species of plants and animals, nature's passive selection has now been superseded by man's active selection. Our task as livestock breeders consists of learning more about the workings of living material, mechanisms of heredity and variation, and of devising systems of breeding and selection so that the inherent possibilities of our stock may have the opportunity to make themselves manifest.

Evidence for Evolution.—Lack of space prevents a lengthy discussion of the various lines of evidence which seem to indicate the validity of the general theory of evolution. In outline, they are as follows:

1. *Classification or Taxonomy.* The fact that all the 800,000 described species of animals can be arranged into 11 phyla and the 250,000 known species of plants into 4 phyla, the whole resembling a branching tree.

2. *Comparative Embryology.* The fact that all embryos start as single-celled zygotes, progress along similar lines of development, and that those

of the higher species pass hurriedly through stages which are the end product of organisms lower down the evolutionary scale.

3. *Comparative Anatomy.* The fact that the brain, heart, and other organs show a progressive development from lower to higher species, that all mammals have the same bony framework, the bones in the flipper of a whale, the wing of a bird, the front leg of a horse, and the arm of a man being similar in general form and articulation.

4. *Vestigial Structures.* The fact that man during his embryonic life develops a set of gill clefts and arches, a tail, and a fairly heavy covering of hair, all of which disappear before birth, and that adult man has ear and tail muscles, an appendix, and many other vestigial structures which are well-developed and functional lower down the animal scale.

5. *Paleontology.* The fact that fossil remains of animals show a progressive development from lower to higher in ascending strata of the earth's crust.

6. *Zoogeography.* The fact that species grow increasingly divergent in form in widening circles from their point of origin.

7. *Blood Tests.* The fact that the blood of closely related animals shows small incompatibilities as measured by amount of precipitation, whereas distantly related ones show great incompatibilities.

8. *Observation and Experiment.* The fact that all of our breeds of farm animals have been made by a process of selection during about the past 200 years and that recently a successful cross was made between the radish and the cabbage giving a true breeding form having some characteristics of both parents but no longer being fertile with either parent.

Evolution of the Horse.—The evolution of the horse is more completely known from fossils than is that of any other species of animal. Evidences of horses are found in both the New and Old Worlds as far back as Eocene time. Loomis, the leading American student of the fossil horse, held that the species arose in Western North America and migrated across what is now Bering Strait into Asia and Europe. They were once populous in South America as well and have been completely wiped out in both continents at different times. Prehistoric horses were very abundant in both North and South America but were not present here when Columbus made his discovery of this continent.

The American representative of Equus in Eocene times was Eohippus. This was a small animal 10 to 20 in. tall, with four toes on the front feet and three toes on the hind feet. The horse representative of the Oligocene was Mesohippus, a three-toed horse, standing about 24 in. high. On through the Miocene, Pliocene, and Pliestocene, the evolutionary process reveals successive adaptations to perpetuate the species from the standpoint of both nutrition and reproduction.

As the horse changes from a denizen of the swamp to that of the forest and later to that of the open prairie, his teeth grow longer, stronger, and more roughened to suit the gradual change to harsher grasses. Accompanying this change comes a great change in the structure of the feet and legs. The cannon bones, metacarpals and metatarsals, lengthen, the middle toe grows larger and stronger, and the other toes gradually disappear. This permits greater and greater speed, on which this species had to depend for survival. In the modern horse, only the middle or third toe remains, with rudiments (splints) of the second and fourth toes. The Eocene horse with four toes recounts the first of these changes. It is confidently hoped the original five-toed horse will one day be discovered. Figure 24 shows the progressive changes in the teeth and forelimbs of the horse from Eohippus to the modern Equus.

Mechanism of Evolution.—Granted living forms, capable of survival and reproduction, and granted relative but not absolute stability, an evolutionary process would seem to be inevitable. The obvious question at this point would appear to be, what is the mechanism of the process, how did it work? The answer logically involves two factors, one the internal features and the other the influence of the external environment.

We have assumed that life originated in minute and relatively simple forms. Because the modern science of genetics has shown that inheritance at the present time depends upon the make-up of the chromosomes, meaning thereby their content of genes, it again seems logical to suppose that this has been the system of inheritance from the very origin of life onward.

We do not at the present moment know the chemical content or structure of any gene. After proper staining, the chromosomes in all the higher species can be readily observed. These bodies always have a definite form and number in each species. They appear superficially to be made up of units strung together much like beads on a string. These individual units are the genes. Studies of the giant chromosomes found in the salivary glands of *Drosophila melanogaster* when in the larval stage have shown that the genes are discrete bodies or regions of the greater whole, the chromosome. Cytological investigations have revealed also that demonstrable departures from the normal in mature pomace flies are correlated with evident changes in the form or arrangement of the discrete units making up the chromosomes, the genes. These and many other features of correspondence between genetic development and cytological form will be discussed later when we discuss the chromosomal theory of inheritance. Suffice it to say here that this evidence has now reached the point where it can no longer be doubted. In other words the modern breeder now has a workable theory of inheritance

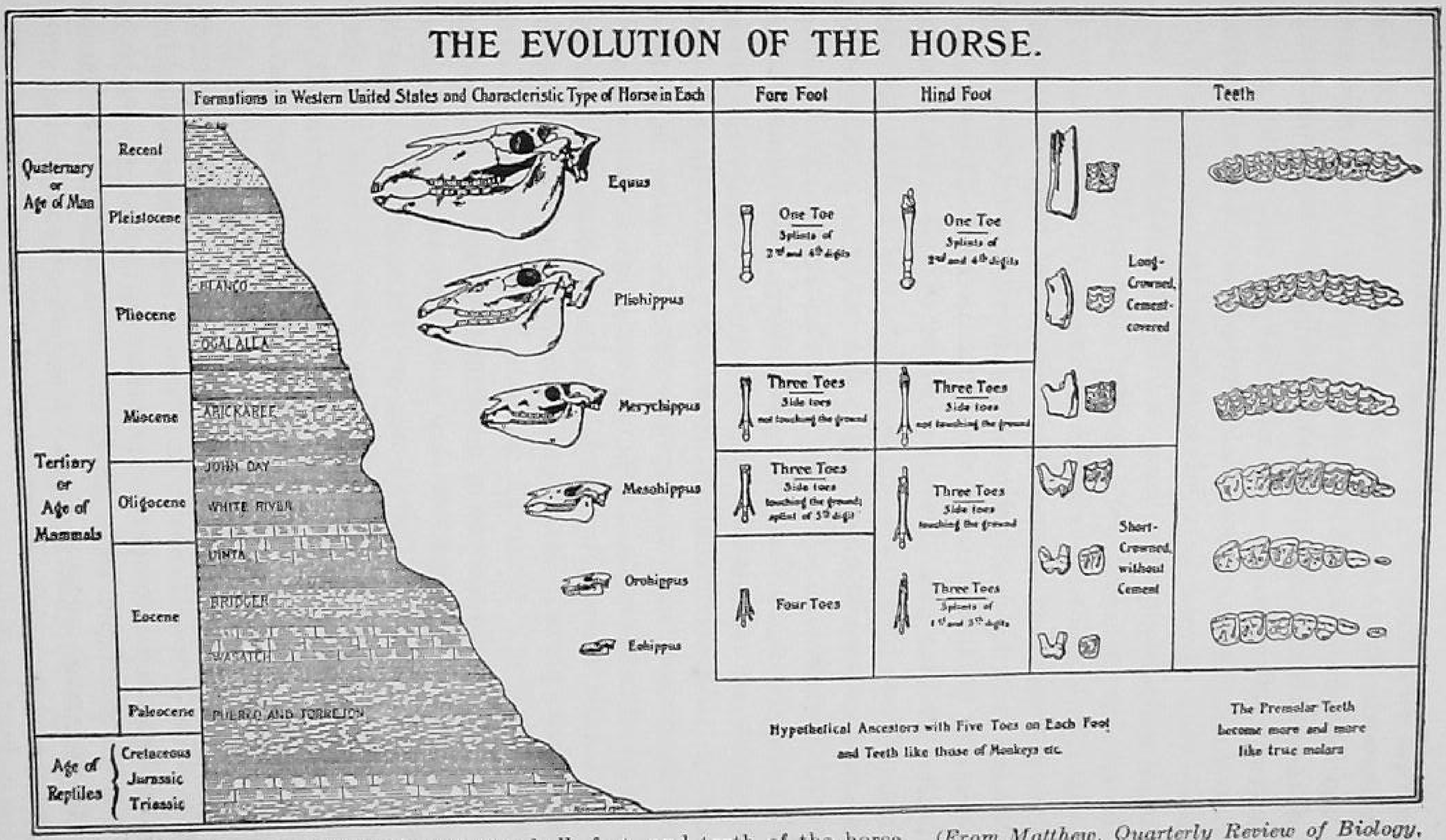

FIG. 24.—Showing progressive changes in skull, feet, and teeth of the horse. (*From Matthew, Quarterly Review of Biology, Williams & Wilkins Company.*)

whose broad outlines appear applicable to all forms of life and whose details have already been worked out in many of the lower, simpler, more rapidly multiplying forms. And this theory rests solidly on the genes as the hereditary units involved in the transmission of potentialities from parent to offspring.

The mechanism of inheritance between individuals today is the gene. The mechanism of evolution, inheritance between all living forms in all time, is undoubtedly also the gene. For this to be true, the gene must be able to reproduce itself exactly. It does this today at every cell division, it has done it billions of times in your own body, it has undoubtedly been doing it since the earliest living forms first appeared. In addition to reproducing itself exactly, the gene must also be capable of occasionally producing some slight change as it reproduces itself. This power has also been demonstrated in today's living forms, and such changes have been given the name *mutations*. There would seem to be no right or necessity for denying this power to living forms from their very inception.

This, in brief form, is the content of modern evolutionary thought. In other words, its mechanism is to be found in changes in the genes. Of necessity, only those changes which were relatively slight would survive. Any living form, from a single gene to a horse, is a very delicately balanced mechanism. Any major change would probably be lethal. A horse's legs might grow a little longer, and, if this little was not too much to prevent the mouth from reaching to the ground, the horse would survive; if too great, it would be handicapped in securing food. Likewise, small changes in genes are possible of survival, large ones probably not. The gene or the horse can adapt itself to small changes, not to large ones. In time, the summation of many small changes would, of course, cause the organism to vary considerably from its original state This will be recognized as the heart of the Darwinian theory of the origin of new forms. It is still the most logical explanation of that process.

The stream of life is, therefore, the germ plasm, and the germ plasm is the sum of the genes. Perhaps the genes existed first as naked bodies, next became grouped into aggregates, next took on cytoplasm to assist in their growing complexity of function. We might liken the whole process to radiating assembly lines. The hub or core is the simplest living form, the gene. One assembly line adds but little material as the genes pass along it, and there eventuates at the end of the line an amoeba. Another adds more and different materials, so that there roll off this line marine forms like fish. Yet another line produces amphibia, another reptiles, another birds, and yet another mammals. The workers

along these assembly lines are the genes, their raw materials chemical elements or compounds, their finished products all the millions of forms of plants and animals that have lived or exist now.

Role of the Environment.—The other feature of this general problem of the mechanism of evolution is concerned with the environment. Various roles have been ascribed to this feature in the past. As noted earlier, Lamarck and others before and since his time have given first place to the environment as the causative factor of variation. That the environment may have been very active in causing variations in the minute and relatively naked early living (germinal) material seems quite probable, after the hereditary material had encased itself in a protective coat of cytoplasm seems less likely. Just where the dividing line may have come is hard to say. Recent research has shown that the germ cells of forms like *D. melanogaster* are highly subject to change due to direct treatment by varying dosages of X rays or of heat. It seems unnecessary to doubt that the relatively better protected germ cells of higher forms might be subject to similar experimental influences, though perhaps to a lessened degree. That the germ cells can be changed by such processes seems well established, that the changes can be induced in an advantageously directed manner is not established. Owing to the delicate balance between any organism and its environment, most of the changes seem to be deleterious rather than beneficial.

The general role of the environment, at least in later stages of the developmental process, seems to have been that of a passive selective agent rather than the direct causative agent. Probably both natural genetic variability and that induced by the environment have functioned from the start. In its earlier stages, changes were perhaps more largely due to the environment; in its later stages, mostly to genetic variations, natural changes in the genes, although for any variation there is presumably some specific cause. This natural genetic mutability is capable of at least two sorts of explanation. Either it is induced by some outside supernatural force, or it is inherent in the relatively unstable nature of the material itself.

The mechanism of inheritance is to be found in the germinal materials, the genes. The process of progressive change is best viewed as that of interactions between the genes and their environment, both cellular and general. In the higher forms, the environment seems to act largely in a passive manner, somewhat perhaps in the nature of a sieve, allowing some varieties better fitted for their particular environment to survive and leave offspring, whereas others are unable to do so. It also seems plausible to think that variations in a certain direction might lead to still others in the same direction, a view known as ortho-

genesis. The last man born arose through a gradual developmental process beginning as one undifferentiated zygote, ending as an organism made up of billions of cells organized into a definite pattern that sets him off from all his fellows as a unique individual. Logic as well as fact, as far as known, dictate that the first man was made by a similar process.

Mechanism of Development.—Any organism, plant or animal, is composed of cells, one, hundreds, thousands, or billions. In the year

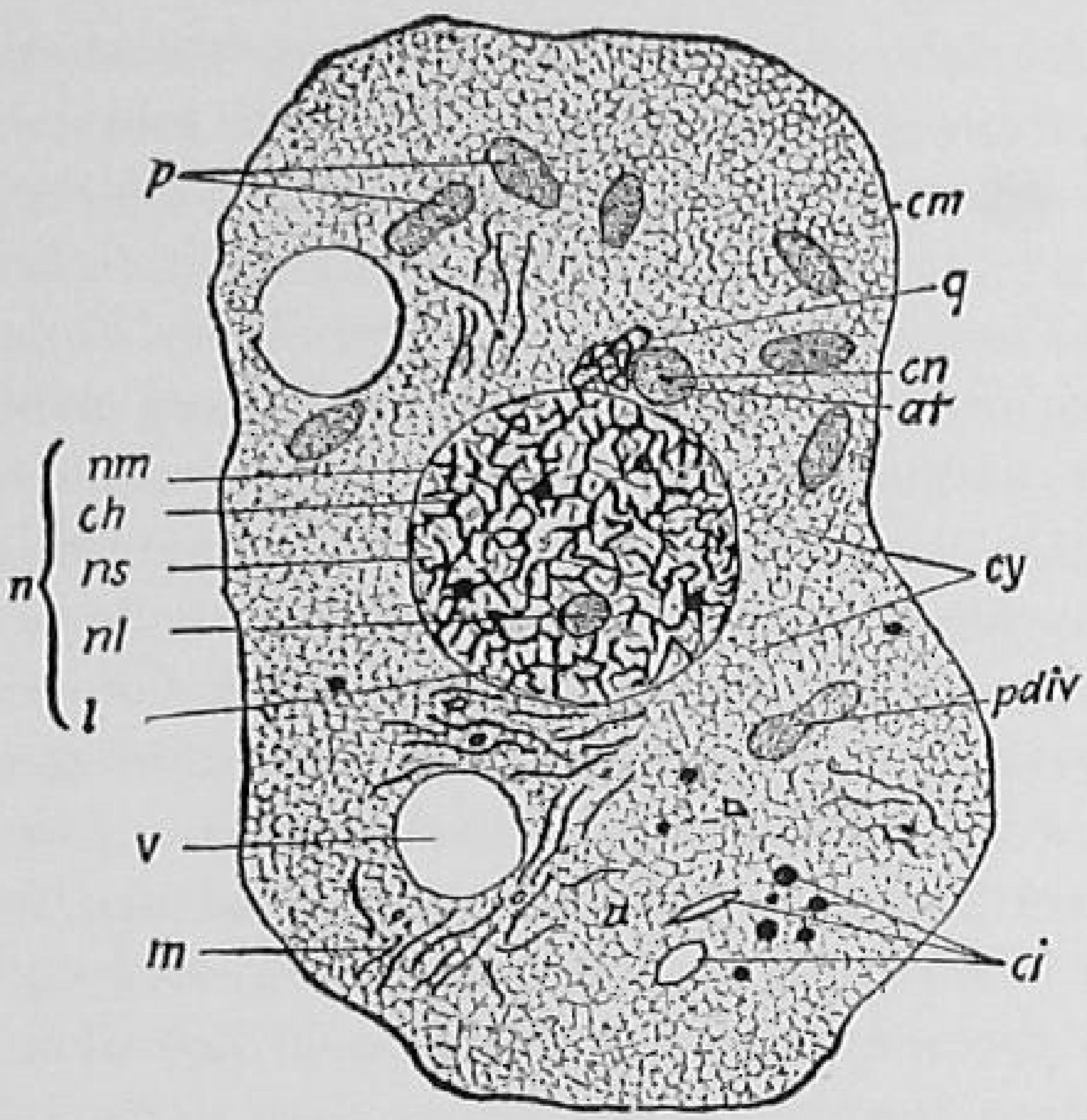

FIG. 25.—Diagram of a typical cell, with structures commonly present. *at*, attraction sphere; *ch*, chromatin network; *ci*, cell inclusions; *cm*, cell membrane; *cn*, centrosome; *cy*, cytoplasm; *l*, linin thread; *n*, nucleus; *nl*, nucleolus; *nm*, nuclear membrane; *ns*, nuclear sap; *p*, plastids; *pdiv*, plastid dividing; *v*, vacuole. (*From Shull, Principles of Animal Biology.*)

1665, Hooke observed the cellular structure of cork. In 1838, two German scientists, Schleiden and Schwann, propounded the cell theory for both plants and animals. In its very briefest form, the cell doctrine states that all plants and animals are made up of units called *cells*. In both the plant and the animal kingdoms are found all degrees of complexity from single-celled organisms, like algae and amoebae, to highly specialized structures, such as plants and farm animals, which consist literally of billions of cells.

A cell is a bit of living protoplasm in which are to be found vacuoles, plastids, a centrosome, and a nucleus, the whole sometimes surrounded by a wall and sometimes naked. The really important part is the content of the cell, the sum total of which is called *protoplasm*. This includes the nucleus, centrosome, and the remaining portion called the *cytoplasm*.

The body of any multicellular organism is made up of cells (and cell products) that have arisen through cell division from one original cell called a *zygote*. The zygote is the product of the union of two reproductive cells, *viz.*, an ovum from the female and a spermatozoon from the male.

Following the fertilization of an ovum by a spermatozoon, the resulting zygote begins to grow by means of cell division. This one original cell divides into two cells, these two into four, etc., until the complete organsim, consisting of billions of cells in the higher animals, is produced. The complex individuals found among the higher animals are composed of a great diversity of kinds of cells that have arisen through specilization. All the organs of an animal body are composed of cells more or less specialized in form and function for definite purposes—lung cells for breathing, brain cells for thinking, etc. Reproduction is likewise affected through the activity of certain specialized cells.

Classification of Cells.—For clarity, and because of certain fundamental differences, the cells making up any organism are grouped into two categories. One of these, called the *somatoplasm*, includes all the cells necessary to the well-being of the particular individual whose component parts they are. The other relates to the cells immediately concerned in the production of future individuals and is called the *germ plasm*. It is essential that the student differentiate clearly between these two. True, the germ cells are housed in and nourished by means of the soma or body cells, but differences in cell division as well as in function place the former in a class by themselves. In farm animals a new individual arises through cell division from a zygote, which is an ovum or egg of the female that has been fertilized by a spermatozoon from the male.

Both ova and spermatozoa are cells with the characteristic cytoplasm and nucleus. The ova are produced in the ovaries of the female. Ova are usually larger than the spermatozoa because of the stored-up food material in the yolk that must serve to nourish the developing individual until the latter becomes firmly attached in the uterus of the mother. The spermatozoa, produced in the testicles of the male, are also specialized for their function of seeking out and fertilizing the ova. They have a characteristic shape, very unlike that of the ova, being made up of three parts, *viz.*, the head, containing the nucleus; the body, containing the centrosome; and the elongated tail, which gives the spermatozoa their motility. The chromosomes found in the nuclei of the germ cells furnish the "bridge of inheritance" between parent and offspring.

Chromosomes and Genes.—The theory was advanced many years ago that certain definite entities in the nucleus of the germ cell brought

about the development of certain characteristics in the fully developed individual. Subsequent investigation in cytology has proved the correctness of this hypothesis. In the higher animals, there is a marked distinction between soma and germ plasm, and also between the cytoplasm and the nucleus of the germ cells. It is in the nucleus that the determiners for the individual's characteristics are located. The nucleus itself is made up of two principal parts, the linin network and the chromatin material. This latter goes through various stages in fulfilling its functions. In a resting state, it is strung out in a long thread supported on the linin network. As the cell starts to divide, the chromatin thread shortens and thickens and, finally, breaks up into the number of chromosomes characteristic of the species.

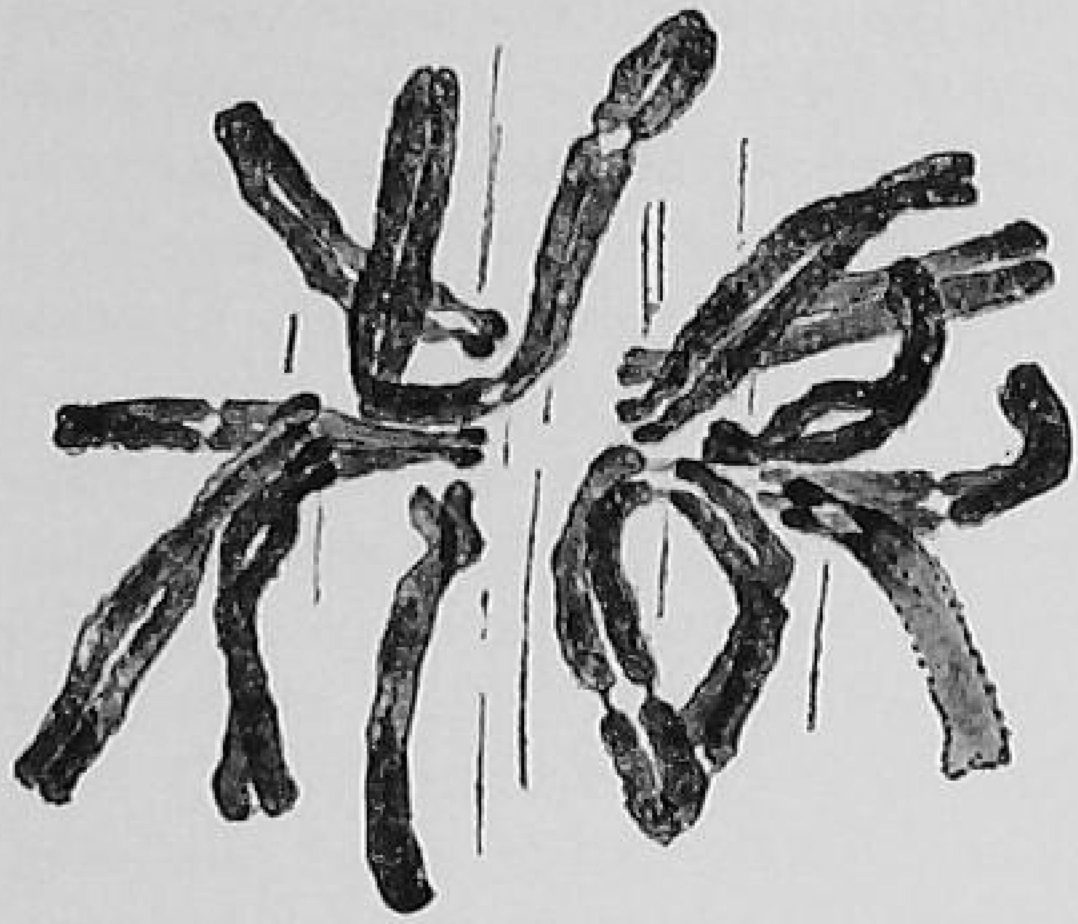

FIG. 26.—Diploid chromosome complement at metaphase in root tip of *Vicia faba*. Spindle-attachment regions of all chromosomes near equator. Nucleolus-forming regions are by the "secondary constrictions" above and below. In this strain one pair of short chromosomes has conspicuous "constrictions" also (left and right). × 1750. (*From Sharp, Introduction to Cytology.*)

Each species of plant and animal has a characteristic number of chromosomes. This number is found in the nuclei of all the cells of the body that have a nucleus, with the exception of the germ cells at certain stages as will be noted later. In the human, the number of chromosomes is 48; in cattle, 60; in Drosophila, 8; in corn, 20; and in wheat, 16. The chromosomes themselves are divided into two categories, *viz.*, autosomes and sex chromosomes, the latter being so named because they carry the principal determiners for sex as well as for certain other characteristics. The chromosomes occur in a variety of shapes, though for the most part they are rodlike or oval in shape. Abundant cytological and experimental breeding data have now been diligently studied, and these data have proved that each chromosome consists of a great many constituents known as genes, which are the indivisible units of inheritance.

It is supposed that certain of the filterable viruses which are assumed to be the causative agents in certain diseases, such as hog cholera, are composed quite largely of nuclear or chromatin material with very little or no cytoplasm present. As indicated above, it seems most probable that life must have originated in somewhat similar minute bodies and that from this minute origin all the varied forms of living things have

arisen by means of heredity and variation. The most logical reason for the differences between individuals would seem to be that their chromatin elements differ. The same is undoubtedly true of species, class, and phyletic differences. During cell division the chromatin becomes stretched out into a long thread, and at more or less regular intervals the thread exhibits regions of thickening. In other words, the chromosomes look like strings of beads. These beads are the genes

TABLE 8.—CHROMOSOME NUMBERS IN MAN AND FARM MAMMALS

Species	Number	Authority
Man	48	Evans and Swezy, 1928
Horse	60	Painter, 1924
Cattle	60	Krallinger, 1927
Sheep	54	Berry, 1938
Swine	38	Krallinger, 1931
Goat	60	Berry, 1938

or factors which bring about the development of all of our individual characteristics. Each chromosome is always reformed from the same group of genes, and each gene always occupies a definite locus on its particular chromosome.

Somatic Mitosis.—Somatic mitosis or cell division is the process whereby one cell, through growth and subsequent division into approximately equal halves, produces two cells. Somatic mitosis is a continuous process starting with one cell in the resting state and ending with two cells in the resting state. For clarity the process is often divided into four phases, as follows: prophase, metaphase, anaphase, and telophase.

In a typical cell in the resting state, the chromatin of the nucleus is strung out into long threads presenting the appearance of a tangled skein. In the prophase, a shortening and thickening of the chromatin and its division into the number of chromosomes characteristic for the species, together with the arrangement of the chromosomes in an equatorial plane, take place. The nuclear wall also disappears during this preparatory stage. By this time the centrosome, which lies just outside the nucleus, has divided, and one-half of it has proceeded to each pole of the cell with the accompanying arrangement of the asters attached to the chromosomes. In the metaphase, the chromosomes split lengthwise (or reproduce themselves) into two equal parts, and these parts start to move to the opposite poles of the cell. In the anaphase, the two groups of chromosomes complete their migration, one group to each pole of the cell. In the telophase, the cell wall constricts, forming two

Fig. 27.—Diagram of mitosis in a four-chromosome species, 1–5, prophase; 6–8, metaphase; 9, anaphase; 10, telophase.

new daughter cells, each with cytoplasm, centrosome, and nucleus with its chromatin, in place of the one original parent cell.

Such cell division with differentiation is characteristic of the rise of a many-celled organism from a single-celled zygote. At times this process stops short and a dwarf results; and at other times it continues beyond the normal, the individual with an extra number of cells being a giant. Various types of abnormalities arise from causes unknown.

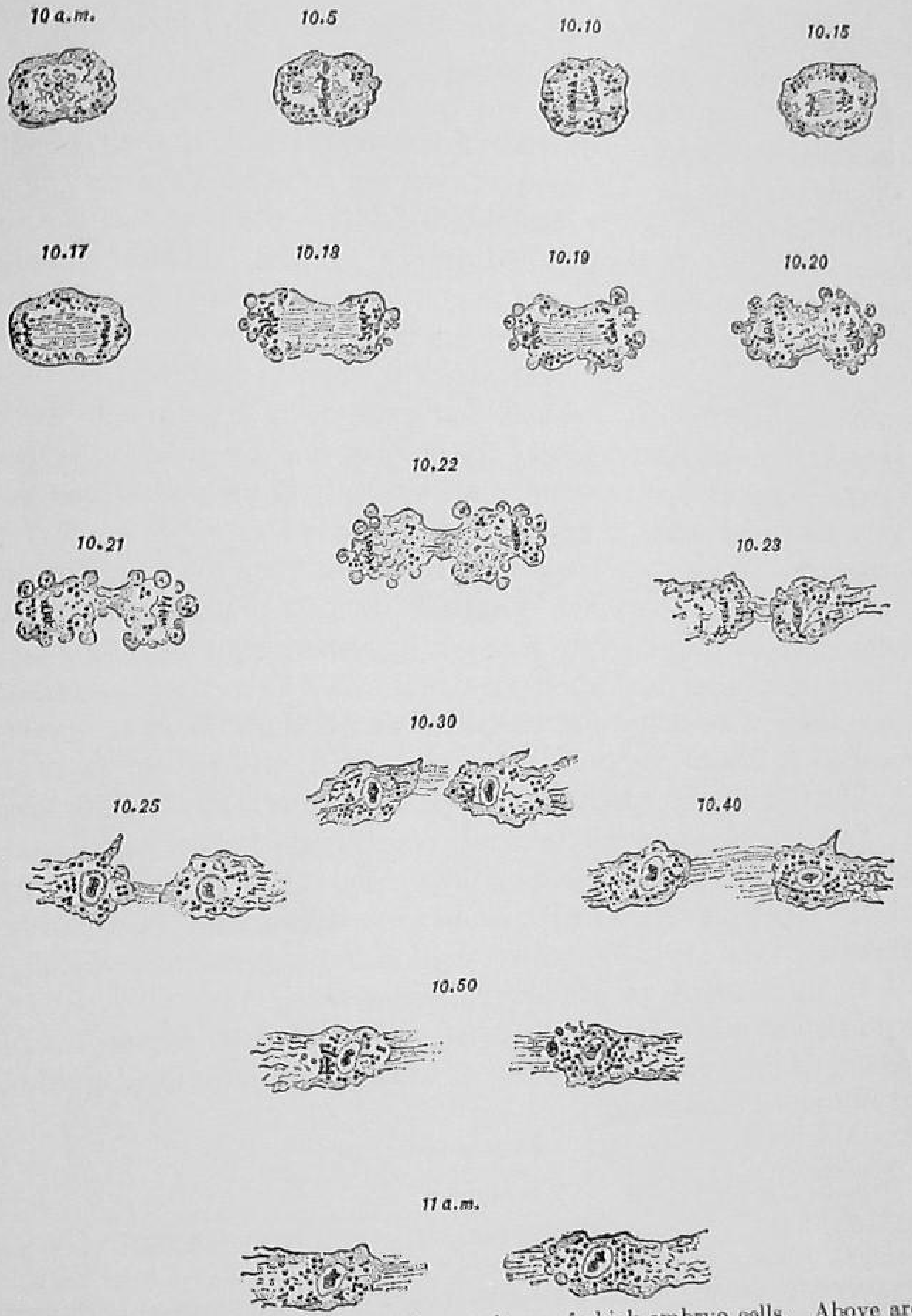

FIG. 28.—The division of a living cell in a culture of chick embryo cells. Above are the times at which the drawings were taken, the whole series representing 1 hour. (*From C. C. Hurst, The Mechanism of Creative Evolution, The Macmillan Company.*)

The force that specifies when, where, and how differentiation is to take place is not definitely known. Perhaps it is the result of response to internal stimuli, perhaps to pressure of other cells, perhaps to the influences of organizing centers. Up to the present, differentiation is still largely a mystery, but the wonder should arise not at the fact that occasionally abnormalities are produced but, rather, that the whole

complicated process from the one to the billions with consequent differentiation is ever accomplished perfectly.

Origin of Germ Cells.—The mechanism of inheritance resides in the germ cells, the only direct contribution of parents to their offspring in the higher species. The mode of origin of germ cells is a very important consideration. As we shall see in detail in the next two chapters, they are produced in testicles and ovaries, but they should be thought of as direct lineal descendants of the fertilized ovum that has also given rise to the entire somatoplasm of the individual now producing germ cells. At sexual maturity, germ cells will begin to be produced by the germ plasm, but the chromosomes and genes in these germ cells are not derived in the final analysis from the body of the parent (somatoplasm) but from the same source from which the body of the parent has come, *viz.*, the fertilized ovum or zygote.

Summary.—We have tried in this chapter to trace the broad outlines of the process of development of animals from its probable inception in ultramicroscopic forms on up through its varied manifestations to its final eventuation in the highest mammals. We have tried to correlate the processes of heredity and variation, as we know them to manifest themselves today in our breeding animals, with the greater process of the production of new species and races. We have seen that life apparently first manifested itself in some very simple forms, and that by means of heredity and variation plus differential survival all the thousands of higher forms have gradually made their appearance in an orderly progression. Thus it has appeared that all living forms are related, or, if not all tracing back to one original living thing, they all must trace back to similar original manifestations of life. Finally, we outlined the process of somatic mitosis by means of which a new individual gradually arises from a fertilized egg.

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SECTION II

Mechanisms of Reproduction

CHAPTER IV

THE MALE'S PART IN REPRODUCTION

The science of physiology seeks to explain the how and the why of all the varied reactions or responses of living organisms to external or internal stimuli and to determine the function of each organ of the body, as well as the interrelations existing among all parts of the body. The physiology of reproduction seeks to explain the part that each of the specialized organs of this system plays in the animal's ability to reproduce its kind.

From the time of the early Greeks on through the Dark Ages, the works of Galen, an anatomist of the second century, served as the authority in anatomical and physiological science. This was in keeping with the general tendency of the time to believe what someone else had said, rather than to question and to seek to test whether what was asserted was actually true. Galen used the method of observation but made his observations on animals alone, applying the results in a general way to man.

In 1315, an Italian professor, Mondino da Luzzi by name, published a work on human anatomy based on dissection of human bodies rather than on Galen's authority. It remained, however, for Vesalius, a Belgian born in 1514, to break the allegiance to old authority and to set up experimental inquiry in its place.

After the establishment of the experimental method, in which Harvey, an Englishman, played a leading part, all that remained needful was the perfection of method. Up to the seventeenth century, restricted progress was all that could be expected, for it was not until then that men such as Hooke and Grew in England, Malpighi in Italy, and Swammerdam and Leeuwenhoek in Holland began to develop compound microscopes for study of minute phenomena of all kinds. Physiology is founded upon the function of organs, but it was not until 1838 that men began to understand even the structure of organs. This development started with the founding of the cell doctrine of Schleiden and Schwann in that year.

Preformation and Incasement.—The older thought and belief regarding reproduction were embodied in the "preformation theory." This

was, in effect, a theory that the whole body with all its parts was already contained in the egg or sperm of an animal but in such a minute and transparent form that it could not be detected and that, therefore, the whole of development was nothing more than a growth, or an unfolding, of the parts that were already "infolded." Closely connected with this theory was that of incasement. According to this theory, the embryonic ovary was supposed to contain the ova of the following generation; these again the ova of the next, etc., ad infinitum.

Early Discoveries in Embryology.—Wolff, in 1759, after careful observations, proved that embryonic development did not consist of an unfolding of the preformed organs but was a series of new constructions, one part arising after another, all of them simple in their early stages, though perhaps highly specialized later. The substantiation of his finding by Oken, in 1806, stimulated activity in the field of embryological research. Baer was the most successful of these investigators. His contribution led to the discovery of the three germinal layers on the germ disk of all the higher animals, *viz.*, the ectoderm, the mesoderm, and the endoderm.

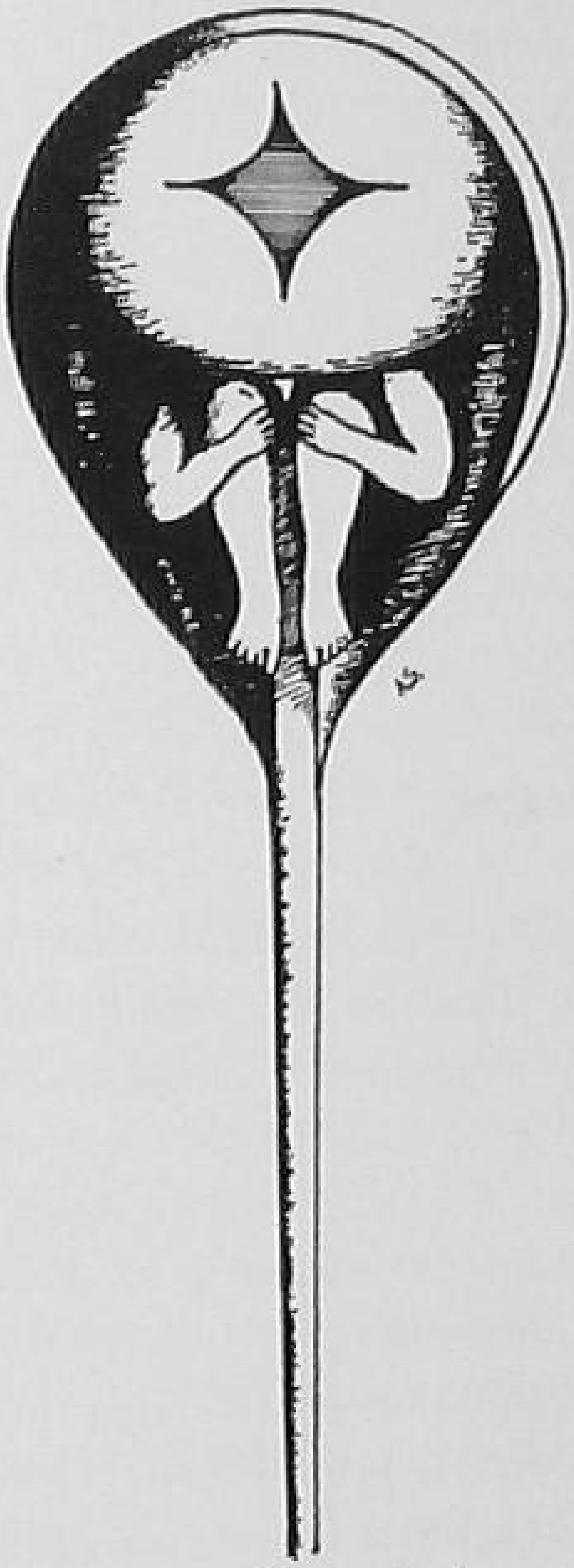


FIG. 29.—Hartsoeker's conception of human sperm in accordance with the theory of preformation (1694).

From the ectoderm arise later the nervous system, important parts of the sense organs, the outer layer of the skin, and some others; from the endoderm, the lining of most of the digestive tract and such outgrowths of the digestive tube as the liver, pancreas, and the lungs; and from the mesoderm, the muscles, bones, blood system, and most of the urogenital system.[1]

Baer also first discovered the human ovum, a tiny cell in the Graafian follicle $1/125$ in. in diameter.

Ten years after Baer had given a firm foundation to embryological science by his theory of germ layers, a new task confronted it on the establishment of the cellular theory, in 1838. What is the relation of the ovum and the layers which arise from it to the tissues and cells which compose the fully developed organism?

[1] HAECKEL, E., "The Riddle of the Universe," p. 58, Harper & Brothers, New York, 1901.

The correct answer to this difficult question was given about the middle of this century by two distinguished pupils of Johannes Müller—Robert Remak, of Berlin, and Albert Kölliker, of Würzburg. They showed that the ovum is at first one simple cell, and that the many germinal globules, or granules, which arise from it by repeated segmentation, are also simple cells. From this mulberrylike group of cells are constructed first the germinal layers, and subsequently, by differentiation or division of labor, all the different organs. Kölliker has the further merit of showing that the seminal fluid of male animals is also a mass of microscopic cells. Thus it was proved that both the materials of generation, the male sperm and the female ova, fell in with the cellular theory.[1]

Forms of Reproduction.—From the standpoint of nature, there are three main considerations for any succession of individuals: (1) The individual must be born, (2) it must grow to maturity, and (3) it must reproduce in order that the cycle may be endless. Reproduction is the most vital consideration in nature. It simply cannot fail, and the adaptations to prevent failure are almost endless.

There are two general types of reproduction, *viz.*, asexual and sexual.

ASEXUAL

Fission. Cell division.

Budding. A small part being pinched off.

Vegetative. Regeneration of a whole from a part.

SEXUAL

Parthenogenesis. Female hatching young from unfertilized eggs.

Paedogenesis. Reproduction by young or larval animals (may be parthenogenetic).

Hermaphroditism. Both sexes in one individual.

Unisexualism. Requiring combined function of two individuals of opposite sex.

In all the higher animals, unisexuality prevails, the union of male and female germ cells, produced by the two separate entities, being necessary for the production of a new individual. All the marvelously specialized organs, in both male and female, for accomplishing this result have had a common origin, and, although the differentiation probably began millions of years ago, there still remain many similarities between the male and the female genitalia. The reproductive organs of one sex have their homologues in the other, although each has been specialized for its respective function. The genital ridge, the first indication of sex organs in the embryo, is much alike in both male and female of the higher species for a considerable time before specialization begins.

[1] *Ibid.*

It will be the purpose in this and the following chapter to study the principles underlying reproductive physiology. It is not the purpose to attempt to develop veterinarians, however desirable that might be from a breeding standpoint, but to impart to the breeder intimate knowledge of the principles underlying reproduction, in order that he may practice his profession wisely and understand and counsel with the veterinarian when it becomes necessary to call upon the latter.

Embryological Development of the Genitalia.—The urogenital system of the higher animals is formed for the most part from mesodermal tissue. This double system, designed both to rid the body of certain waste products and to provide a means for reproducing the species, has had a very interesting evolutionary development.

The earliest stage in this development results in the formation of the paired pronephric tubules, or pronephros. This is the functional kidney in Amphioxus and some lampreys. It forms in 7 to 14 somites toward the cephalic end of the embryo from the intermediate cell mass of the mesodermal somite (nephrotome). Mesially this forms an invagination opening into the coelom, with which blood vessels communicate and waste products transfuse into these invaginated areas. The free or distal end of this section of each of these somites canalizes, the tubular ends bend backward, anastomose, and form a duct that runs posteriorly and empties into the cloaca, the pronephric duct. These structures are found in early embryonic stages of larval fishes, amphibians, reptiles, birds, and mammals but are transitional.

The second kidney formed is the mesonephros. As the primitive pronephric tubules degenerate, there are formed behind them about 80 mesonephric tubules that empty into the already formed pronephric duct. This second formation is known as the *mesonephros* or *Wolffian body* and serves the higher organism as a temporary excretory organ, although in man it is entirely degenerate in a four-month embryo. The old pronephric duct is now called the *mesonephric* or *Wolffian duct.* For some larval fish and amphibians, the mesonephros is the permanent kidney.

The true kidney is the third stage in this evolutionary process. The ureter and collecting tubules of the permanent kidney grow out from the caudal end of the mesonephric duct, while the secretory tubules and Bowman's capsule are formed from the caudal end of the nephrogenic cord.

The growth of these tissues in the successive somites of the early embryo causes a longitudinal ridge known as the *urogenital ridge* to form in the body cavity on either side of the median line. This ridge soon divides into a lateral mesonephric fold and a median genital fold. In the former are located the Wolffian duct, already spoken of, and there later forms,

by invagination, another hollow tube, the Müllerian duct. The mesial portion of the urogenital fold—the genital fold—is of peculiar interest because it is destined to form either testicles or ovaries. This genital fold in the early weeks of embryonic life extends from near the diaphragm back toward the posterior end of the embryo. Later the anterior portion of the body grows relatively faster, so that the fold assumes a more caudal position, and this together with differential growth causes the genital fold to assume a beanlike shape. Thus are formed the gonads, or precursors of testes and ovaries.

The human embryo, therefore, at six weeks has a pair of undifferentiated gonads and two sets of tubes, Wolffian and Müllerian. Its sex has been previously determined by the chromosome content of the egg and sperm, but there has as yet been no differentiation of specific male or female parts. Such differentiation begins to be noticeable at about six weeks when the embryo is about $\frac{1}{3}$ to $\frac{1}{2}$ in. in length.

If the embryo is destined to become a male, the gonads complete their development into testes, which pass down into the pelvic cavity and about a month before birth into the scrotum. The Wolffian duct (old pronephric) differentiates into the long, variously differentiated tube which will eventually carry the spermatozoa from the testes out through the penis. The Müllerian duct on the other hand atrophies and, except for two small vestiges (at the top of the testicle and embedded in the prostate gland), disappears.

If the embryo is destined to become a female, the gonads develop into ovaries, the Müllerian duct into the uterine tubes, uterus, cervix, and part of the vagina, while the Wolffian duct, again except for two small nonfunctional vestiges in the ovary, disappears. In some cases the sex-differentiating mechanism fails to function properly and varying incomplete stages of both sexes appear in the individual, popularly, but erroneously, called *hermaphrodites*.

The gonad consists of a central core of connective tissue, or stroma, with blood vessels and nerves and is covered with a layer of germinal epithelium. Columns of cells (Pflügers egg cords) from the germinal epithelium grow down into the stroma. In the male these cords give rise to the convoluted seminiferous tubules that after birth canalize into tubules in which the spermatozoa eventually are formed. The sustentacular cells of Sertoli, or nurse cells, are formed within the tubules from the undifferentiated epithelial cells of the sex cords, while the interstitial cells that lie outside and around the tubules are formed from the mesenchymal stroma. After the fifth week, a dense layer of connective tissue, the tunica albuginea, develops between the germinal

epithelium and the sex cords, and the epithelium is reduced to a single layer of flat cells.

In the female the process is very similar, except that the first group of egg cords seems to disappear, after which another group of egg cords passes down into the stroma of the ovary. These egg cords break up and form the many thousands of immature follicles that are present in the ovaries at birth.

It is seen from the above that the primordial germ cells are present in an embryo at a very early age. Granted normal health, there is nothing that a breeder can do to change them or their hereditary units in any way. From a genetic point of view, an animal will transmit just the same when it is a two-year-old as when it is a ten-year-old. We can trace these early germ cells' precursors in the embryonic testes or ovaries back to the original fertilized egg or zygote that gave rise to this particular embryo. It is seen, therefore, that the manner in which an animal will transmit is determined very early, actually when the specific egg was fertilized by the specific sperm to produce this specific animal. The new being got certain determiners of hereditary characteristics from both of its parents. At sexual maturity, it will be ready to pass on a sample half of this hereditary material to each of its offspring. After fertilization has once taken place, the breeder is powerless to change the genetic make-up of the developing fetus. His only chance for animal improvement comes before this event, and his task is to devise ways of learning the genetic content of the germ cells of his animals so that he may know what he actually has from a genetic standpoint in the animals in his herd or flock.

The genital tubercle develops in the mid-line between the umbilical cord and anus at about the third or fourth week of embryonic life. On its caudal slope there appears a small urethral groove. In the male this groove closes over, and it eventually extends all the way through the penis and the glans. Rounded ridges (labio-scrotal swellings) appear on each side of the base of the phallus and in the male hollow out to form the two-chambered scrotum or sac in which the testes are carried. In the female the phallus lags in development and eventually forms the clitoris, while the labio-scrotal swellings form the labia majora, or external lips of the vulva.

The Testis.—In mammals, with the exception of the whale, elephant, rhinoceros, and seal which do not have scrota, the testes are present in the scrotum at or shortly following birth. Their basic anatomy is established during embryonic and fetal development, but their functional development awaits the proper environmental and endocrine stimulation. The testis is covered by a dense connective-tissue capsule, the tunica

albuginea, from which connective-tissue extensions, the septa, radiate and divide the testis into lobules. Within each lobule are the seminiferous tubules, long coiled ducts in which the spermatozoa will eventually be produced. The seminiferous tubules converge at the apexes of the lobules where they straighten out and become the tubuli recti, and in

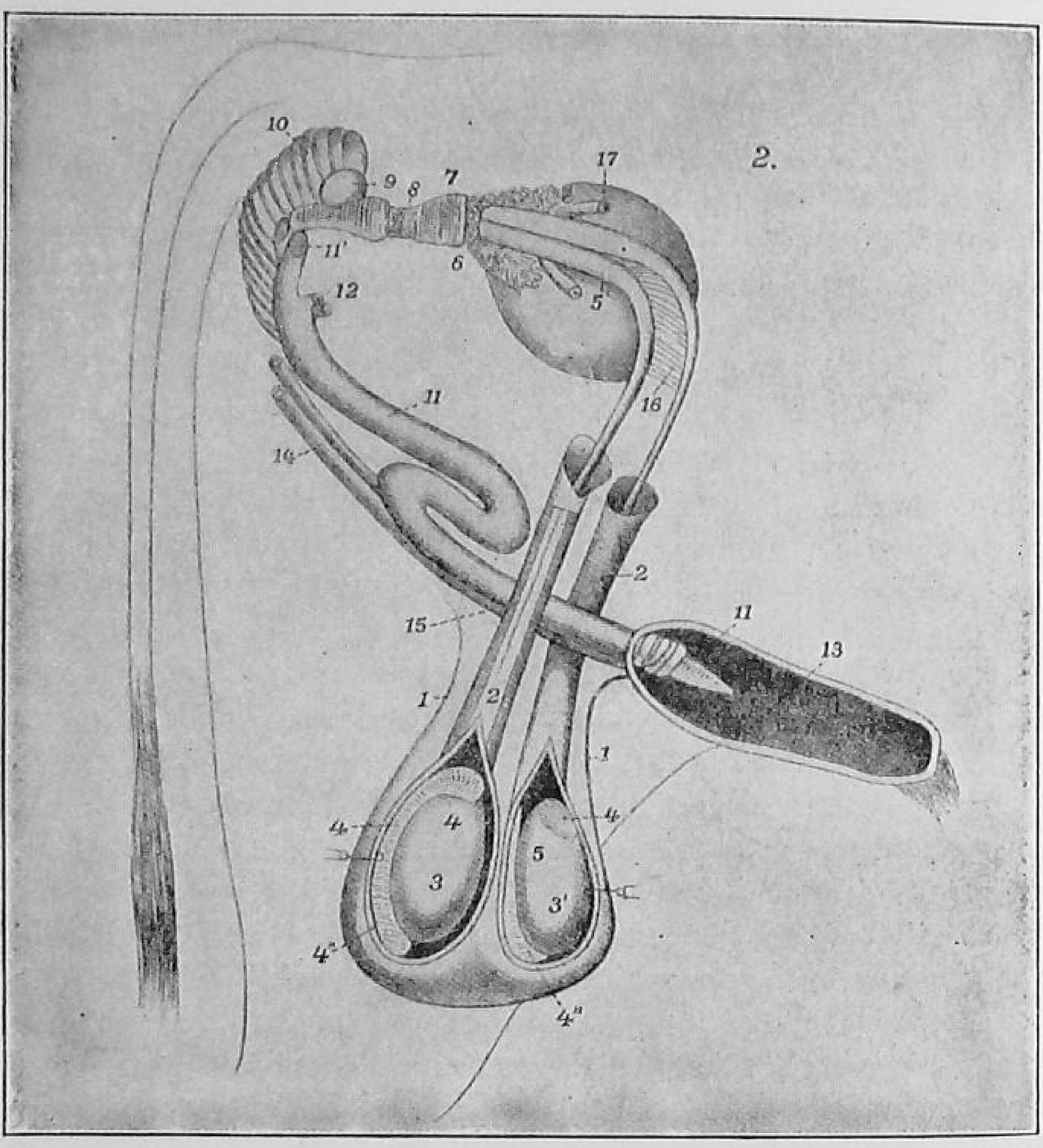


FIG. 30.—Generative and urinary organs of bull. 1, scrotum; 2, spermatic chord; 3, testicle; 4, epididymis (globus major and minor); 5, vas deferens; 6, vesicula seminalis; 7, membranous portion of urethral canal covered by Wilson's muscle; 8, part of prostate gland covered by Wilson's muscle; 9, Cowper's gland; 10, accelerator urinae muscle; 11, penis; 12, cut suspensory ligaments of penis; 13, sheath, laid open; 17, ureters. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

turn enter the rete testis, a system of irregular anastomosing cavernous spaces. From the rete testis there is a series of ductules (about 20 in man) which emerge on the surface of the testis and enter the head of the epididymis. Around and between the seminiferous tubules there are numerous blood vessels, nerves, and connective tissue and the interstitial or Leydig cells.

The testis has two distinct functions. The older, phylogenetically, is probably the production of spermatozoa. This function is carried on in the seminiferous tubules. The second function is the production of the male hormone, testosterone. The male hormone is necessary for the development and function of the male genital organs and for such secondary sexual characteristics as sexual drive. facial hair in the human, and

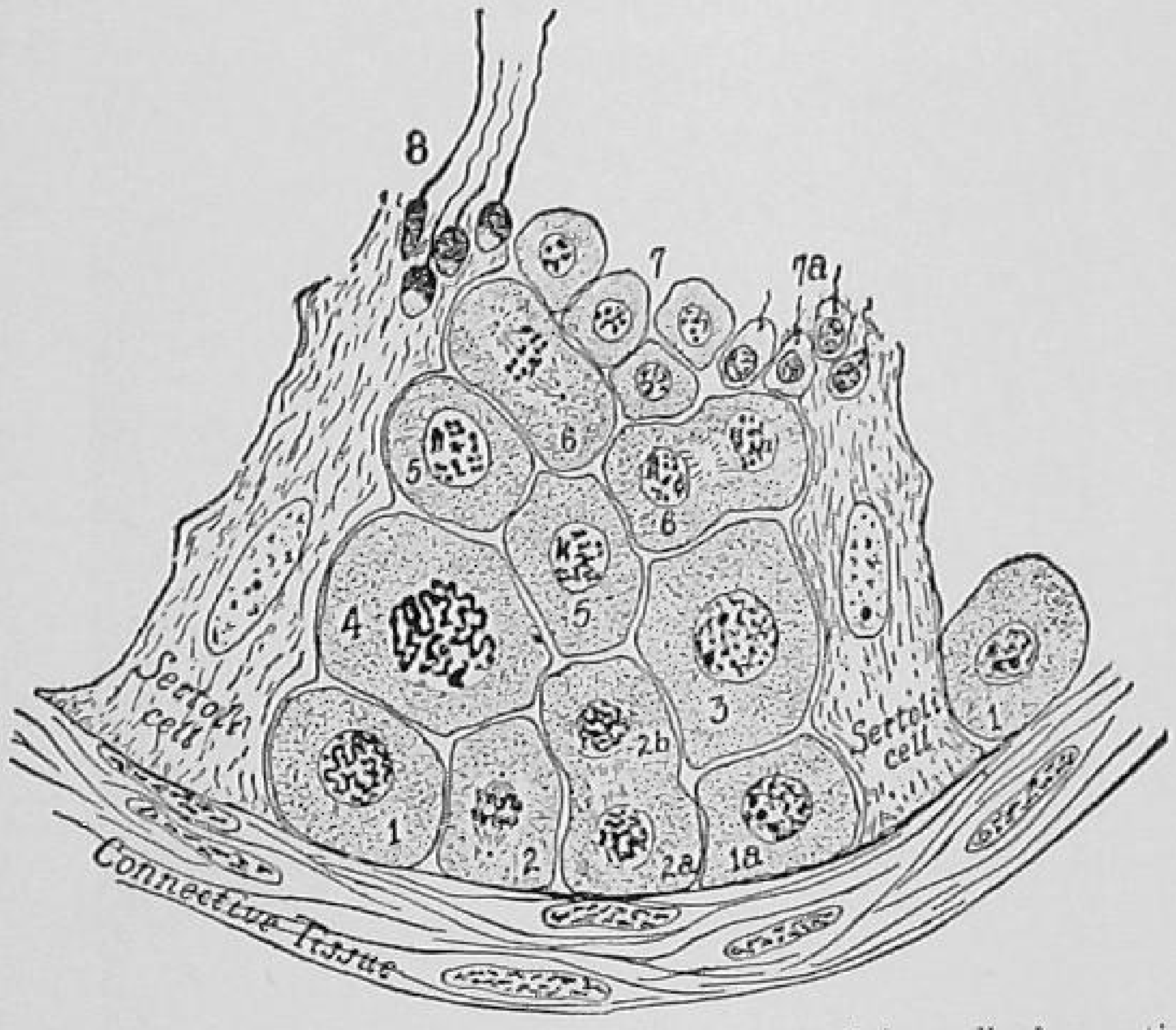


FIG. 31.—Semischematic figure showing small segment of the wall of an active seminiferous tubule. The sequence of events in the production of spermia is indicated by the numbers. A spermatogonium (1) goes into mitosis (2) producing two daughter cells (2*a* and 2*b*). One daughter cell (2*a*) may remain peripherally located as a new spermatogonium eventually coming to occupy such a position as 1*a*. The other daughter cell (2*b*) may grow into a primary spermatocyte (3) being crowded meanwhile nearer the lumen of the tubule. When fully grown the primary spermatocyte will go into mitosis again (4) and produce two secondary spermatocytes (5, 5). Each secondary spermatocyte at once divides again (6, 6) producing spermatids (7). The spermatids become embedded in the tip of a Sertoli cell 7*a*), there undergoing their metamorphosis and becoming spermia (8), which when mature are detached into the lumen of the seminiferous tubule. (*From Patten, Embryology of the Pig, 2d ed., The Blakiston Company.*)

the brilliant feather patterns of some birds. The hormonal function is carried on by the interstitial cells.

The mature active testis is a very busy and efficient organ. Since millions and even billions of sperm are ejaculated at each copulation, the surface area of the germinal epithelium is necessarily large. It has been estimated that the seminiferous tubules of man, if laid end to end, would extend about 1,000 ft. and in the bull nearly 3 mi. At birth the seminiferous tubules contain a basal layer of loosely arranged cells called the spermatogonia and the Sertoli or nurse cells to which the sperm will

temporarily attach themselves during the final stages of development. There is no central canal in the tubules at this time. As sexual development progresses, the spermatogonia divide by ordinary mitosis and form primary spermatocytes from which are derived secondary spermatocytes, spermatids, and spermatozoa in their proper turn. As this process progresses, the testis increases in size, the seminiferous tubules increase in diameter, a central canal appears in each tubule, and the

FIG. 32.—Seminiferous tubule of mature rat testis. Observe the almost diagrammatic arrangement of the cells and the abundance of all cell types.

sperm eventually pass through the tubuli recti into the rete testis, the efferent ducts, and thence to the epididymis.

In order that the number of chromosomes typical of the species may be maintained, and yet a means of variation provided, sperm proliferation is accompanied by a process called miosis. The spermatogonia, or sperm mother cells, grow and enlarge and may divide to form either other spermatogonia or primary spermatocytes. The spermatogonium remains at the wall of the tubule, while the other, the primary spermatocyte, begins to move toward the lumen. This latter cell goes through two rapid cell divisions. Previous to the first cell division, synapsis (fusing of like members of pairs of chromosomes) occurs.

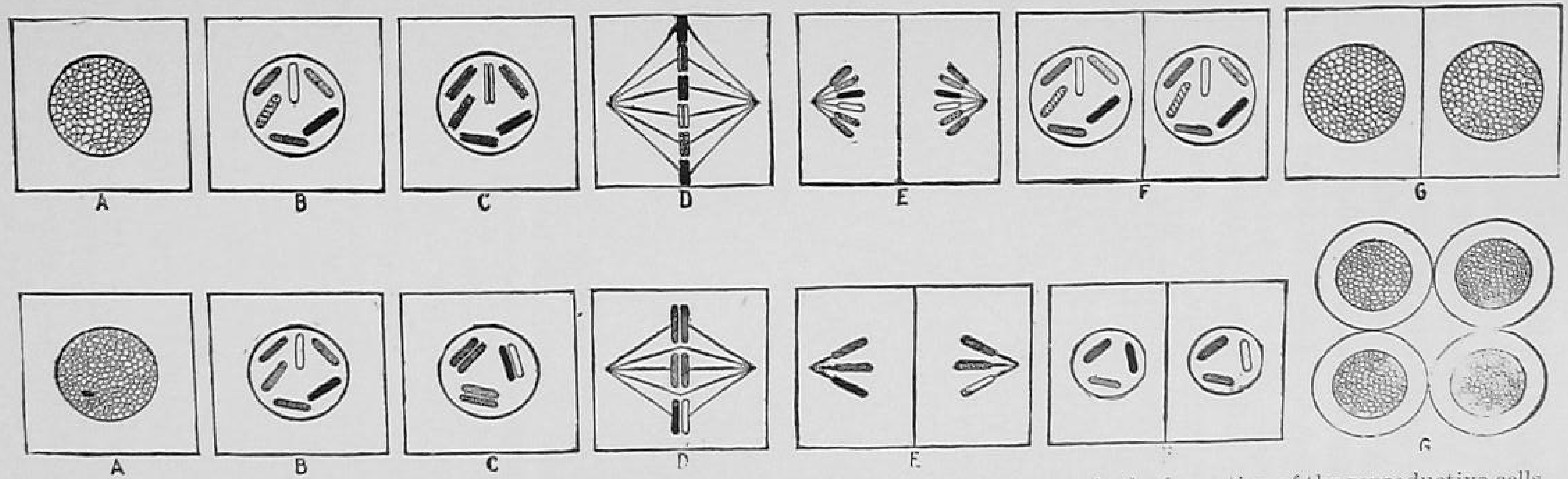


FIG. 33.—Comparison between mitosis in the body cells and in the miotic divisions which precede the formation of the reproductive cells. The individual chromosomes are differently marked. In ordinary mitosis (upper row) it is evident that the chromatin is divided equally between the two daughter cells (*F* left and right). In the reduction divisions (lower row) the chromosomes do not split but align themselves in pairs (*C* and *D*), and one member of each pair goes to each pole (*E*), resulting in the formation of two cells (*F*), each with half as many chromosomes as the body cells. These by a subsequent mitosis give rise to four functional gametes (*G*). (*After Sinnott and Dunn, modified from Sharp.*)

During synapsis each of the fused homologous chromosomes splits or reproduces, each one thus coming to consist of two sister chromatids, making a bundle of four chromatids, or the tetrad. The paired chromatids twist about each other at this time, and sometimes a section of a chromatid is replaced by a section from one of the members of the homologous pair of sister chromatids. This interchange of chromatin material between nonsister chromatids will be discussed fully in a later chapter when we are dealing with crossing over.

Synapsis is followed by disjunction of the fused pairs of chromatids, one pair now moving to each of the two poles of the cell. Upon the completion of this migration of chromatids, the cell wall constricts, forming two secondary spermatocytes, each with one-half the normal

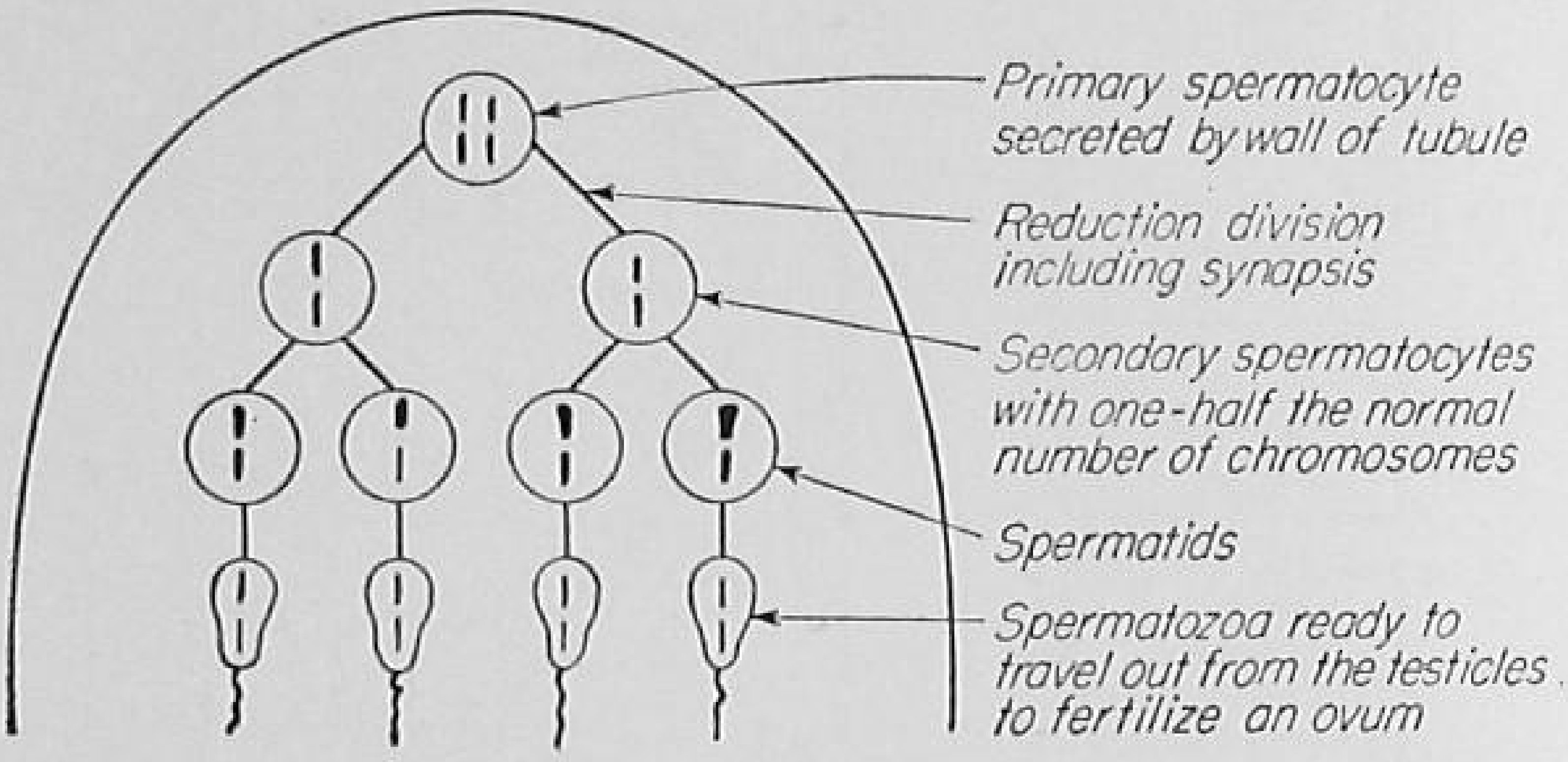


FIG. 34.—Schematic seminiferous tubule showing spermatogenesis.

number of chromosomes for the particular species, each in the form of a fused pair of chromatids. This division is spoken of as the *heterotypic division*, because the two resulting cells are not identical with the parent cell. The two secondary spermatocytes now go through a homotypic division, one of each of the original four chromatids being found in each of the resulting four spermatids. The spermatids in turn become elongated, the nucleus passes to one end, and the opposite end stretches out into a long filamentous tail, the lashing of which provides the sperm with its motility. The newly formed spermatozoa then become attached to the large nurse or Sertoli cells, which project toward the lumen of the seminiferous tubules. The fully developed spermatozoa are found eventually in the lumina of the tubules through which they make their exit from the testes.

Hormonal Regulation of the Testis.—The primary regulating agents of the testis are the gonadotropic hormones produced by the anterior pituitary gland. If these hormones fail to be produced in sufficient amounts in the young animal, sexual maturity does not occur. Failure

of gonadotropic hormone production in the mature animal is followed by both spermatogenic and endocrine dysfunction of the testis. There are two gonadotropic hormones. One is called the follicle-stimulating hormone (FSH) and the other the luteinizing hormone (LH). These gonadotropins also regulate ovarian function, and their names are actually descriptive of their effects in the female. Some workers refer to the luteinizing hormone as the interstitial-cell-stimulating hormone (ICSH). Both hormones are proteins and have been isolated from the anterior pituitary in relatively pure form. Both FSH and LH produce enlarge-

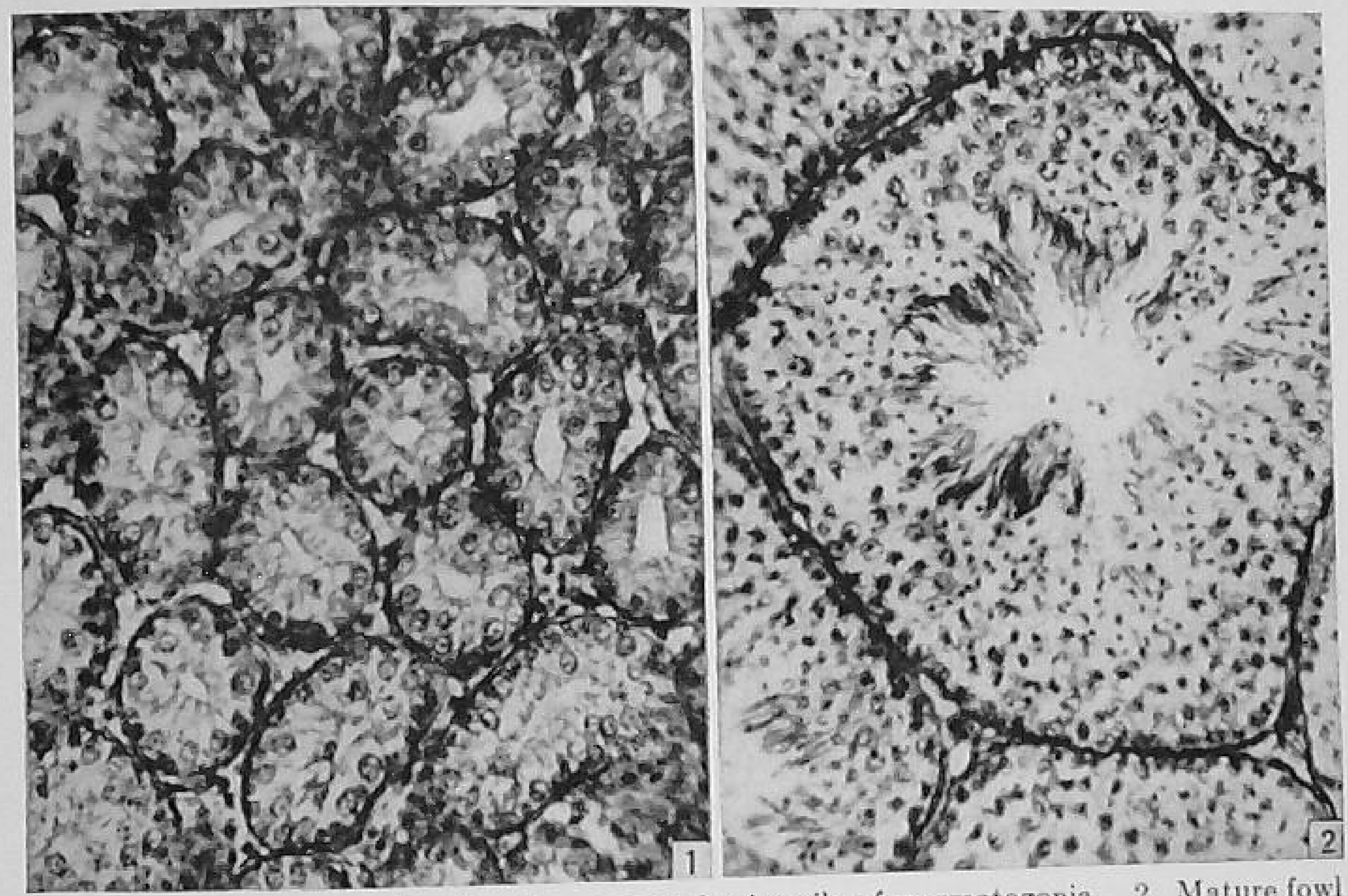


FIG. 35.—1. Immature fowl testis, composed primarily of spermatogonia. 2. Mature fowl testis showing abundant germinal cells of all types including sperm.

ment of the testis when injected, but each acts in a different manner. The development and maintenance of the seminiferous tubules and spermatogenesis are dependent primarily on FSH. The interstitial cells of the testis, which secrete the male hormone, are stimulated by LH. Although the male hormone is concerned chiefly with the accessory structures of the male genitalia and the secondary sexual characteristics, it may also assist in the development and function of the seminiferous tubules. Thus it appears that the normal development of the seminiferous tubules depends upon FSH, LH, and the male hormone.

Age and Testis Function.—There are wide species, strain, and individual differences in the age at which spermatozoa are produced. Studies at the Purdue Experiment Station (Hogue and Schnetzler, 1937) showed that in the chicken full spermatogenesis was attained between the

eighteenth and thirtieth weeks and was then maintained more or less continuously throughout reproductive life. The pattern of spermatogenesis was somewhat different in the ring-necked pheasant, a species which normally breeds in the spring. It was found that in some males the testes contained sperm at about fourteen weeks of age but that the testes then regressed to a resting stage until spring. Full spermatogenesis was thus not attained until the males were about forty weeks of age (Kirkpatrick and Andrews, 1944). Phillips and Andrews (1936) found that sperm were present in bull testes at thirty-two weeks and in the boar at twenty-one weeks. The testes of purebred, inbred, crossbred, and hybrid boars have been studied at Purdue (Andrews *et al.*, 1949). Sperm were consistently present in one of the Duroc lines as early as 110 days and in another line did not appear regularly until 140 days. The age at which sexual maturity occurs is of considerable importance in the development of new lines of breeding. Delayed or incomplete spermatogenesis may reflect itself in lowered prolificacy and fertility. Precocious sexual maturity may interfere with the growth process, for the production of large amounts of the male or androgenic hormone may cause the long bones to cease growing at too early an age.

Seasonal Periodicity.—In most birds in this hemisphere the production of both sperm and ova is strictly a seasonal phenomenon. The chicken, however, has been carefully selected on the basis of reproductive capacity for many years and is now regarded as a continuous breeder. Wheeler and Andrews (1943) have shown, however, that in the Barred Rock the greatest numbers of sperm per ejaculate are produced between December and April. The domestic turkey and goose are definitely seasonal breeders. In the majority of mammals sperm are produced only at certain seasons of the year. Seasonal spermatogenesis is characteristic of wild species, but man and the domesticated mammals have long been regarded as continuous breeders. Only in recent years has it been recognized that there are seasonal differences in the rate of spermatogenesis or in semen quality, even though sperm are produced throughout the entire year. It is assumed by many that sexual drive is indicative of the degree of spermatogenesis and, for example, that the willingness of rams to mate throughout the year is an indication that sperm are being produced. This is not true, since sperm are formed in the seminiferous tubules, a region which is anatomically separate from the hormone-secreting portion of the testis. Sexual drive can be stimulated in the castrate male by the injection of the androgenic hormone, but it is impossible for such an animal to produce sperm. McKenzie and Berliner (1937) clearly showed that in the ram, under normal Missouri conditions, spermatogenesis and semen quality were maximum in the fall and minimum in July

and August. Shropshire rams were more affected by season than Hampshires.

A 20-year study of breeding efficiency in the Purdue dairy herd showed that fertility was maximum in March, April, May, and June and minimum in July, August, and February. Part of this seasonal difference was attributed to the effect of season on semen quality (Erb *et al.*, 1942). The lowest conception rate was obtained in the winter and spring in three herds of cattle located at different latitudes in eastern Canada, and the highest fertility occurred in the summer and fall (Mercier and Salisbury, 1947). A companion study of the seasonal variations in fertility of 125,000 cows and 71 bulls in New York State showed that younger and older cattle were most affected by season. The poorest conception rate was observed in the winter. It was concluded that the amount of daylight had a definite influence on fertility at that latitude and that the response to light varied with the age of the animal (Mercier and Salisbury, 1947).

Effect of Light and Temperature.—The most obvious characteristics of the seasons are differences in light, temperature, and in some areas, precipitation. Plants are especially responsive to these variations, and florists make routine use of controlled light and temperature in the production of out-of-season crops. Animals are probably not quite so responsive to light as plants. However, the ancient Chinese are reported to have known that canaries could be induced to sing out of season if candles were placed in front of their cages. We know now that singing was induced because of the stimulatory effects of light on sexual activity. Rowan's (1929) work with the junco clearly showed that sperm production could be brought about in November and December by increasing the length of day, even though the birds were at the same time subjected to subzero temperatures. The normal mating season of the junco is in May. Poultrymen have long made use of artificial light to alter patterns of egg production. It is generally agreed that in chickens artificial light usually does not increase the total number of eggs but makes possible their production at a time of year when eggs are most valuable (fall and winter). Turkeys can be induced to produce both eggs and sperm earlier in the winter than normal by the use of supplementary illumination. The effects of quality of light are incompletely known. Bissonnette (1931) found that white and red light were most effective and that green light inhibited testis function in the starling.

It is obviously more difficult to alter the environment of the larger farm animals and the effects of light on spermatogenesis are incompletely known. As previously pointed out, the seasonal differences in fertility of cattle may be explained on the basis of light at some latitudes.

The effects of temperature on spermatogenesis are probably subject to wide species variations. In birds, including the domestic fowl, it is probably correct to generalize that light has much more effect on spermatogenesis than temperature. McKenzie and Berliner reported a marked decline in semen quality when rams were placed in a warm room during the winter. Mills (1939) has summarized data on seasonal variations on human conception rate in various North American cities. In San Francisco, where there is very little seasonal variation in temperature, there are practically no monthly fluctuations in conception rate. In Tampa, Fla., and Charleston, S.C., there are significantly fewer conceptions in July and August. Mills points out that human fertility is maximum when the mean monthly temperature is between 40 and 65°F. Fertility declines when the mean temperature rises above 70°F. or falls below 40°F. In most parts of the United States high environmental temperatures coincide with maximum length of day, and it thus becomes difficult to separate the effects of the two on animals maintained under normal conditions.

It is clear that environmental alteration does affect the reproductive process. The mode of action of the external environmental factors is at least partially understood. The removal of the anterior pituitary gland brings about a complete cessation of either testicular or ovarian activity and seasonal reproductive cycles cease. The injection of the anterior pituitary gonadotropic hormones reestablishes gonad activity. It appears, therefore, that the anterior pituitary is the chief regulating agent. The several possibilities by which environmental factors may influence gonad function have been summarized by Turner (1948). In some species, the ferret, the optic nerve must be intact if light is to affect the anterior pituitary, whereas in the duck the optic nerve is not essential. There are marked seasonal differences in general metabolism which may conceivably affect the gonads directly or indirectly by means of the anterior pituitary. Body heat production rises as environmental temperature declines. Much of this is due to changes in activity of the thyroid gland. In the human it has long been known that both hypo- and hyperthyroidism are associated with lowered fertility, and there is evidence that this may also be true of farm animals. Reineke (1946) found that thyroprotein, a compound which contains the thyroid hormone thyroxine, will correct certain types of infertility in bulls, and Shaffner and Andrews (1948) reported that experimental hypothyroidism reduced semen quality in the fowl.

The effects of season upon the quality of feedstuffs and general plane of nutrition should not be overlooked. It is perhaps not a coincidence that fertility is highest during the months when pastures are most luxuri-

ant. Throughout much of the United States the nutritive status of animals declines during the late winter months, and the stimulating effects of spring pastures on milk production, growth, fertility, and general health are well known. This is due to the fact that some of the constituents of feeds, *e.g.*, vitamin A, deteriorate during storage. Vitamin A is essential for normal fertility, and pasture is one of the richest source of this vitamin.

The Hormonal Functions of the Testis.—As previously stated, the testis is concerned with the production of spermatozoa and the secretion of the male hormone by the interstitial or Leydig cells. Although the testicular hormone was not identified chemically until 1935, Berthold had suggested as early as 1849 that the testis produced a substance which was responsible for the development of the secondary sexual characteristics. The term *male hormone* is a broad one and is not limited to a specific compound. Although occasional reports have been made that the testis produces more than one hormone, the best evidence available indicates that only one is secreted by the testis itself. This testicular hormone is called *testosterone* and is the most potent of the male hormones. The male hormones as a group are called the *androgens* or androgenic hormones. Testosterone, then, is a specific androgen and is produced by the testis. The androgens are widely distributed in animal cells and secretions. Androsterone, an androgen about one-sixth as potent physiologically as testosterone, is usually present in significant amounts in the urine of males. Androgens can also be produced by the ovaries and the adrenal cortex. In the human female it is not uncommon for the adrenals to secrete excessive amounts of androgens and for such male characteristics as facial hair to develop. In the hen it is not unusual for rather marked male secondary sexual changes to occur. Extensive comb growth, crowing, and male sexual behavior may be observed. These are due to increased androgen production, the source of which is usually the rudimentary ovary of the fowl, or the adrenal cortex. It is thus clear that the androgens are not limited to one sex, that tissues other than

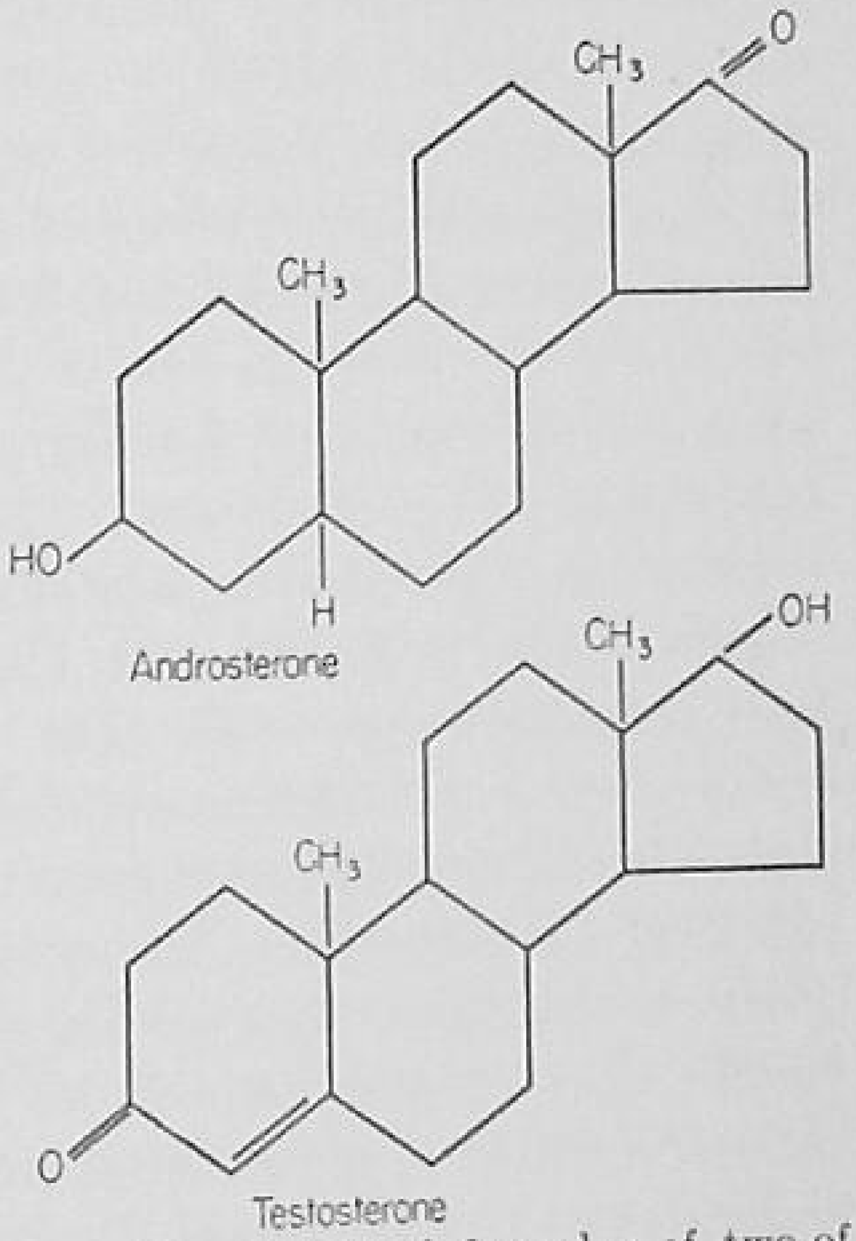


FIG. 36.—Structural formulas of two of the most common male hormones.

the testis can produce them, and that the physiologic and anatomic manifestations of sex may differ from the genetic sex of the individual. Many androgens which do not appear as such in the body have been synthesized in the laboratory.

In the intact organism, hormones are usually secreted by highly specialized cells and are distributed by means of the blood and lymph to other parts of the body where they produce their specific effects. In general terms, the functions of the various hormones are to provide a means of chemical coordination of the tissues and organs which make up the organism as a whole. Testosterone enters the capillaries which supply the interstitial cells and is transported to all body cells. Some of these cells are very responsive to this particular hormone, *e.g.*, the comb of the cock, and tissues such as those found in the small intestine are little affected. Exogenous androgens can be very effective if properly administered. Most of the male hormone compounds are relatively ineffective if administered orally. The most effective methods of administration are the subcutaneous injection of the androgen in oil solution or in the form of dense pellets which can be implanted beneath the skin.

The Male Hormones and Secondary Sexual Characteristics.—The androgens have many functions and somewhat diverse effects in the normal male. In general, the effects of the male hormones are exactly opposite to the changes which occur following castration. The testicular hormone is essential for the normal growth, development, and function of the male genital organs. The seminal vesicles, prostate and Cowper's glands are dependent on this hormone. Without it they undergo very little development and produce relatively little secretion. The growth of the penis, the process of erection, and the development and maintenance of the scrotum are all regulated by the androgens.

Sexual behavior, sex drive or libido, is dependent to a large extent on the androgens. In man and the common farm animals sex drive is present more or less continuously from puberty until senescence. As previously explained, the presence of sex drive does not indicate that sperm are being produced. The ability to copulate is not necessarily lost following castration. The psychological explanation for this is that behavior patterns, when once established, are not immediately lost even when their physiological basis is changed. However, in species which are strictly seasonal breeders, hormonal and spermatogenic activity of the testes are closely correlated and sexual drive is seasonal in nature.

It has long been known that the characteristic male and female secondary sexual characteristics are dependent upon the gonads, since these characters fail to develop following prepubertal castration. The secondary sex characters are highly developed and have been much studied in

birds. In some species, the English sparrow, the feather patterns are not altered by castration or androgen injection. In the domestic fowl genetic and hormonal factors are both involved and in general the male plumage is dependent upon the male hormone. The tusks of the boar, horns and crest of the bull, horns of the ram, and comb of the cock are either reduced in size or lacking if castration is performed at an early age. Neither masculinity nor femininity are absolute. The physiologist explains this partially on the basis of relative differences in the sex hormones, the psychologist on the basis of training and experience, and the geneticist on the basis of gene composition. Whatever the mechanism, there is agreement that sex is relative. The ox is a much more tractable animal than the bull, and this knowledge has been made use of for centuries. The eunuch is characterized by a high-pitched voice, a small chest, beardless face, and is often described as lacking in aggressiveness and intellect.

Miscellaneous Effects of the Male Hormone.—Hundreds of studies on the effects of the androgens on various tissues and body functions have been made. A few of the many effects of these compounds are therefore mentioned. The androgens both stimulate and inhibit general body growth. The effects vary with species and level of hormone dosage. They may increase metabolic rate, increase red-blood cell formation in castrate males, be concerned with pigmentation of the skin, baldness, fat-deposition patterns, nervousness, and numerous other conditions. They have been used experimentally in the treatment of such diverse diseases as angina pectoris, cancer, mastitis, and ringworm of the scalp. It is not implied that the androgens have primary effects in the situations mentioned but that the chemical regulation of the organism by hormones is truly a complex mechanism.

Castration.—The removal of the testes is one of the oldest of surgical procedures. In ancient times, men destined for the priesthood were castrated and prisoners of war and the vanquished were often thus treated. The effects of castration depend somewhat on the age at which the operation is performed. Prepubertal castration of the farm animals produces: (1) permanent sterility, (2) increased skeletal development due to prolonged growth of the long bones, (3) failure of normal development of the genital organs, (4) absence or retardation of the secondary sexual characteristics, (5) improved carcass quality because of increased fat deposition and retardation of such characters as heavy shoulders and neck, (6) absence or retardation of sex drive, (7) varying psychic changes depending upon the species involved. After sexual and body growth have been attained, the outward evidences of castration may be less marked. The most usual effects are (1) atrophy of the genital organs,

(2) loss or diminution of libido, (3) increased fat deposition, (4) decreased basal metabolic rate, and (5) decreased aggressiveness.

The term *castration* implies the surgical removal of the testes; however, several methods of securing the effects of castration without the removal of the gonads are now practiced by livestock men. The most common method in complete removal is to incise or remove the lower portion of the scrotum and then remove the testes. In Europe, and in parts of the United States, castration is frequently performed with a type of instrument called the Burdizzo forceps. These are double-hinged pincers capable of great pressure and are made in various sizes depending on the type of animal involved. One spermatic cord at a time is located in the scrotum and placed between the forceps without cutting the scrotum. When pressure is applied, the spermatic cord and vas deferens are severed by crushing. When properly done, this method is very effective. The testicle immediately begins to atrophy because its blood supply has been cut off and all the effects of castration are produced. This method is called bloodless castration because the scrotum remains intact. Infection is rare and difficulties with flies are avoided. A new method, called elastration, was introduced to the United States from Australia in 1947. Castration is accomplished by placing a special heavy elastic band around the scrotum of lambs at a few days of age. The pressure cuts off the blood supply to the testes and scrotal tip, and both atrophy. This method is reported to have been favorably received by Western sheepmen.

The castration of lambs and pigs by conventional methods is a simple procedure and should be carried out by stockmen at the proper time. The problem is more difficult in cattle and colts and should be performed by a veterinarian, unless the owner has thoroughly learned the art.

The cardinal features are (1) sanitation: clean hands, clean instruments, and clean premises; (2) incisions which are large enough and located so as to ensure complete drainage of the wound; (3) the complete removal of both testes; (4) prevention of excessive loss of blood; (5) proper restraint of the animal; (6) the prevention of undue excitement of the animal.

Lambs are easily castrated by cutting off the tip of the scrotum with a knife or large pair of shears. When pressure is applied to the scrotum, the testes are easily grasped. In young lambs they are best removed by pulling with gentle pressure until the spermatic cord breaks. Pigs are usually held on their backs by an attendant. Two incisions the length of the scrotum about ½ in. from the median lines are made, the testes squeezed out and removed by pulling until the cord breaks. Cutting the spermatic cord with a sharp knife will cause excessive bleeding. In young

animals it is best severed by traction. In older animals it should be crushed with an emasculatome.

If recently castrated animals are confined to dirty premises, infection, sometimes tetanus, may occur. In warm weather a fly repellant should be used.

Lambs and pigs are usually castrated at two to four weeks of age, calves at six to twelve weeks, and colts at about one year of age.

Scrotum.—The testes are formed in the abdominal cavity, and in some species remain there throughout life. In the course of evolutionary development they gradually came to lie at the posterior end of the body pressing against the body wall. A continuation of this process finally led to an outpouching at this region forming a sac, the scrotum, outside the body proper. It is here that the testicles are found in mammalian farm animals. In many other animals (*e.g.*, birds) they remain in the abdominal cavity permanently, whereas still others (*e.g.*, woodchuck) show an intermediate phase with the testicles descending into the scrotum during the breeding or rutting season and being withdrawn into the body cavity when this season is completed.

In addition to serving as a covering for the testicles, the scrotum also functions as a thermoregulatory mechanism. This function of the scrotum is shown by actual differences in temperature, as demonstrated by Moore and Quick (1924) and Phillips and McKenzie (1934), the temperature in the scrotum being from 1 to 8°C. lower than that of the abdominal cavity. It has been shown by several workers that insulation or the application of heat to the testicles results in a degeneration of the spermatogenetic tissue, the production of abnormal sperm, and temporary sterility. These results are also known to follow periods of intense fever. Experimental transposition of the testes to the abdominal cavity leads to the same result, and it has been shown that cooling of the abdomen after transposing the testicles retards the rate of spermatogenic degeneration. If this degeneration has not been too severe or prolonged, the testicles recover their spermatogenic function when all conditions return to normal. Moderate lowering of the temperature of the testicles has been shown to have no deleterious effect on spermatogenesis.

The thermoregulatory function of the scrotum is accomplished through the medium of the tunica dartos muscle, as shown by Phillips and McKenzie (1934). This muscular coat consists of fibroelastic and smooth muscle and consists of two layers, an outer layer applied closely to the skin of the scrotum and a heavier inner layer. This muscle is highly sensitive to changes in temperature, drawing the testicles close up to the body at low temperatures and reversing the process at high temperatures. As shown by Phillips and Andrews (1936) the development of the dartos

anatomically and physiologically parallels the development of the testes, especially their spermatogenic development. Work at Purdue has shown that castration of prepubertal rats prevents the development of the thermoregulatory function, and castration of mature rats is followed by the loss of the function (Tyrell *et al.*, 1942). The injection of testosterone either produced or maintained the thermoregulatory function, depending on the age at which castration was performed (Almquist and Andrews, 1944).

In other words, the gradual transition of the incompletely developed seminiferous tubules of a newborn animal into fully formed tubules endowed with the power of producing mature viable spermatozoa, which occurs during the first few months post partum, is accompanied by the development of the dartos and its transition into a functional mechanism for keeping the temperature of the testicles within physiologically desirable bounds.

If the testicles remain in the abdominal cavity in any species where they should normally descend into the scrotum, a condition known as cryptorchidism, they usually lack their spermatogenic function but retain their endocrine function. In some animals, *e.g.*, the elephant and the anteater, the testicles remain in the abdominal cavity; whereas in others, *e.g.*, most of the rodents and the hedgehog, they descend periodically during the breeding season into the scrotum, whence they are again withdrawn into the abdominal cavity at the end of the breeding season. In the stallion, bull, boar, and ram the testicles communicate through the inguinal canal with the pelvic cavity, where the accessory organs and the glands are located.

Any malformation of the genital organs should be regarded as a serious or disqualifying defect of a herd sire. If an animal is bilaterally cryptorchid, he will usually be sterile. Fertility may be relatively normal if one testis is present in the scrotum. It is well known that cryptorchidism can be inherited, therefore any animal with this characteristic, or from a line where cryptorchidism is prevalent, should not be used for breeding purposes. In commercial livestock production, the occurrence of cryptorchidism increases the difficulties of castration, results in decreased carcass quality when one of the testes is missed at the time of castration, and decreases the value of purebred animals that otherwise might be sold as breeders.

Sometimes the inguinal canal fails to close properly and allows the viscera to enter the scrotum. This condition is known as scrotal hernia and is known to be heritable.

Epididymis.—The convoluted seminiferous tubules converge at the mediastinum testis (absent in Equidae) and there join severally to form

from 6 to 24 efferent ducts. These in turn unite into one duct, thus giving rise to the epididymis, a greatly coiled tube varying from a few feet to several hundred feet in length in some species. The epididymis is lined with tall columnar, ciliated epithelial cells surrounded by a muscular wall, and this in turn is covered by the serosa. One arises near the top of each testis where it is coiled to form the *head* of the epididymis. It eventually passes down the side of the testis, in a part called the *body*, to the bottom of the testis where it forms the *tail* of the epididymis. This tube continues the passageway for the egress of spermatozoa from the seminiferous tubules. The passage of sperm through the epididymis requires 4 to 7 days in the rabbit and 5 to 6 days in the ram (Anderson, 1945). It appears that passage is accomplished by the ciliated cells in the vasa efferentia and epididymis, by testicular pressure and by contractions of these structures which occur during ejaculation.

It is well known that spermatozoa recovered from the testis do not have the same capacity to fertilize ova which sperm in the vas deferens have. The work of Young (1929) clearly showed that a process of maturation of the spermatozoa occurs in the epididymis. Sperm recovered from the head of the epididymis produced approximately half as many conceptions as those taken from the tail region. Many studies on epididymal function have been conducted in recent years. It is generally agreed that the epididymis provides the most favorable medium for the maintenance of sperm viability. The accumulation of harmful metabolites is apparently at a minimum, and the reaction is such that the sperm mature and remain in a resting state until ejaculated. It has been reported by several investigators that epididymal bull sperm are more resistant to cold shock than are ejaculated spermatozoa (Lasley and Mayer, 1944). The functions of the epididymis are (1) a passage and storage place for sperm, (2) the secretion of a small amount of fluid which contributes to the semen, (3) maturation of the spermatozoa. The maintenance of normal epididymal function is dependent upon the presence of the testis hormone. In the absence of the testes, epididymal sperm have a reduced length of life as measured by the maintenance of sperm motility.

Vasa deferentia.—These tubes are a continuation of the epididymides, continuing the passage for the spermatozoa to the urethra. The walls of the vasa deferentia are thick and consist of layers of mucosa, submucosa, muscularis, and fibrosa or serosa. The lumina are small, giving the tubes a firm cordlike character. They are lined with ciliated columnar epithelial cells. In some species there is an enlargement (ampulla of Henle) near the termination of each vas deferens. This is absent in the boar, quite small in the dog and cat, and large in the bull, ram, and

being over 1 in. in diameter and often exceeding 6 in. in length in Equidae. Glands of the vas deferens add to the total content of the semen. The vas deferens, together with longitudinal strands of smooth muscle, blood vessels, and nerves all encased in a fibrous sheath make up the spermatic cord (two of them) that passes up through the inguinal canal into the pelvic cavity.

Sterility can be produced by cutting or tying the vasa deferentia. This operation, vasectomy, is legalized in some states for the sterilization of the feeble-minded, criminally insane, and certain other conditions. Sterility results because sperm are prevented from entering the urethra. Spermatogenesis continues in the testes and the hormonal function is normal. Because some glands, *e.g.*, the pancreas, atrophy if their excurrent ducts are closed, it was hypothesized that following vasectomy sperm formation would eventually cease. It was likewise reasoned that the atrophy of the seminiferous tubules would allow the interstitial cells to produce more hormone and that sexual rejuvenation could be brought about. Information which would tend to disprove this was available as early as 1830, but the so-called rejuvenating operation was widely performed in Europe in the 1930's. Experiments on many species have clearly shown that sperm formation does not cease. The sperm which are produced undergo resorption within the seminiferous tubules and the epididymis.

Ejaculatory Ducts.—These are formed through a union of the vas deferens and the proximal portion of the seminal vesicle on each side. They open into the floor of the urethra through small slitlike apertures between which is found, in man, the uterus masculinus, which is the homologue of the uterus and vagina of the female. In some species, *e.g.*, the boar, there are separate openings for the vasa deferentia and the seminal vesicles into the urethra. On the floor of the prostatic portion of the urethra is found a small elevation known as the crista urethra, or caput gallinaginis, which contains erectile tissues and thus prevents the semen from passing backward into the bladder at time of service.

Seminal Vesicles.—These are the largest of the accessory glands of reproduction in the male. They are located in the pelvic cavity at the ends of the vasa deferentia, being an outgrowth of the latter at their urethral end, and each connects with the urethra by means of a duct.

McKenzie, Miller, and Baugess (1938) report as follows[1] on the seminal vesicles of the boar:

> The glands are tortuous, elongated, hollow bodies, with very irregular, branched lumina and numerous out-pocketings. The wall consists of a thin external con-

[1] McKenzie, F. F., Miller, J. C., and Baugess, L. C., The Reproductive Organs and Semen of The Boar, *Mo. Agr. Expt. Sta. Bul.* 279, 1938, p. 36.

> nective tissue sheet, of a thin middle layer of muscle, and of a mucous membrane resting upon a thin submucous layer. The mucous membrane forms an elaborate system of thin, high primary folds which branch into secondary and tertiary folds. These project far into the lumen, anastomosing frequently with one another, thereby forming many irregularly shaped cavities of different sizes. These cavities are separated from one another by thin branching partitions, and all opening into a larger cavity.
>
> The epithelium lies on a thin vascularized connective tissue supported by muscle strands. Although showing some variation, the epithelium is simple columnar in nature with some areas pseudostratified. The nuclei are round or oval shaped and located at or near the base. Secretion granules are present above the nuclei and on the free surface, drops or bulblike formations appear. These are cast into the lumen, forming the secretion product. The fluid has a gray, opaque color, a medium viscosity, and a pH of approximately 6.7.
>
> There is no central duct of the seminal vesicles. Instead, there are several large ducts branching and anastomosing irregularly, which finally converge into one excretory duct. The duct from each seminal vesicle enters the urethra as a slit-like opening, close to, but ventro-lateral to the vasa openings.

The seminal vesicles vary in size according to the animal and the species, being in the horse 6 to 8 in. long and about 2 in. in diameter. They are lacking in the dog and cat. The function of the seminal vesicles, although not fully understood, is thought to be the secretion of a fluid that furnishes a medium for transport of the spermatozoa. This secretion is thick, alkaline, and globulin-containing. The vesicles were formerly thought to serve as a storage place for spermatozoa, hence their name, but this theory has been disproved. The seminal vesicles are not essential for reproduction as evidenced by the fact that their removal does not produce sterility.

Prostate.—At the neck of the bladder, surrounding or nearly surrounding the urethra and connecting with it by two rows of openings on either side of the ejaculatory ducts, is the prostate gland. This gland is a composite of many small compound tubuloalveolar branching glands. McKenzie *et al.* (1938) studied the prostate in the boar[1] and wrote:

> The prostate gland in the boar is a yellowish multilobular gland. It is composed of two parts; the body or bulb, closely attached to the dorso-lateral surface of the pelvic urethra at its anterior extremity, and the pars disseminata which is attached to the body but embedded in the wall of the pelvic urethra beneath the body of the gland. The body of the gland weighs from 15 to 25 grams and measures about 5 cm. in length by 4 cm. across by 0.5 cm. thick. The ratio of prostate body weight to the live weight of the animals was about 1:8,000.

[1] *Ibid.*, p. 42.

The glandular tissue is firm, without apparent storage space and contains no secretion which can be expelled by pressure. Incomplete sections which have not been made in a known direction, present a bewildering mass of secretory tubules, follicles, connective tissue, smooth muscles, blood vessels, nerves and lymphatics. The gland is a composite of many small compound tubulo-alveolar glands, giving rise to numerous excretory ducts which open into the urethra independently on its dorsal wall.

The prostate is very irregular in form. Large branching cavities, narrow ducts, and alveoli appear to be massed together in an irregular manner. There is no distinct basement membrane and the glandular epithelium rests upon a layer of connective tissue. The epithelium varies from simple or pseudostratified columnar in the smaller alveoli to cuboidal or even squamous in the larger cavities. Numerous secretory granules can be seen in the cytoplasm, and cytoplasmic drops appear to be attached to the free end of the epithelial cells.

There is abundant interstitial tissue which appears to consist of dense connective tissue with collagenous fibers and elastic network, and many smooth muscles arranged in strands of varying thickness. There is also a connective tissue capsule about the periphery of the gland.

The secretion of the prostate is viscid and contains proteins and salts. The prostatic secretion is alkaline, tends to cleanse the urethra prior to and at the time of ejaculation, and provides bulk and a suitable medium for transportation of the spermatozoa. In some animals (rodents) the abundant secretion of the seminal vesicles is coagulated in the vagina by an enzyme in the prostatic fluid, and thus the ejaculate of the male becomes a more or less solid plug in the vagina of the female.

Cowper's Glands.—Cowper's glands (bulbo-urethral), two in number and corresponding to the glands of Bartholin in woman, are situated in the urethral muscle (except in the boar) on either side of the pelvic portion of the urethra, with which each communicates by means of a small duct. They are lacking in the dog and very greatly developed in the boar, a species in which they may extend the entire length of the pelvic floor and reach a diameter of 1½ in. The function of these glands and the urethral glands is thought to be that of producing an alkaline secretion for the purpose of neutralizing and cleansing the urethra before the passage through it of the main bulk of the semen.

Penis.—The remaining portion of the male genitalia consists of the penis. This organ, besides conveying urine to the exterior, has the additional function of conveying spermatozoa into the female genital tract. The penis is made up of muscular and erectile tissue that becomes engorged with blood during the process of erection.

Farm animals exhibit a wide variation in the structure of this organ. In the horse, the end of the penis is rounded, and the organ nearly fills the vagina at copulation. In the bull, the diameter is much smaller, with

the external urethral orifice situated in the urethral papilla at the end and on the left side. The urethral papilla of the bull represents a vestigial filiform appendage. This is well developed in the ram in the form of a slender appendage, which protrudes beyond the glans penis in a twisted manner. The penis of the boar is not provided with an appendage or lateral papilla, and the opening to the exterior is situated at the end of the organ and in the center.

Friction on the glans penis or on the homologue in the female, the clitoris, finally leads to a sexual orgasm during copulation that is in part a reflex action, for it can take place after the spinal cord has been transected. Ejaculation by the male is effected by a series of muscular contractions beginning in the vasa efferentia and involving the epididymis, vasa deferentia, seminal vesicles, prostate, and Cowper's glands. The final discharge of the semen is brought about by the rhythmical contractions of the bulbocavernosus and ischiocavernosus muscles, which, proceeding progressively in waves, result in the ejaculation of the semen from the external orifice of the penis.

Now, in résumé, it may be said that the essential organs of reproduction in the male are the testes, whose functions are to produce spermatozoa and the male hormone; the accessory glands, the prostate, the seminal vesicles, the Cowper's glands, whose function it is to furnish a medium for the spermatozoa to travel in on their way to impregnate the female; and the epididymides, vasa deferentia, and urethra, the parts of a long tube that is concerned with the maturation and passage of the spermatozoa. The blood vessels, nerves, and muscles function in bringing about erection and ejaculation.

Physicochemical Properties of Semen.—Semen is the entire discharge of the male during normal ejaculation. It consists of two general portions. The cellular elements, the spermatozoa, are produced by the testis. The liquid portion of the semen, the plasma, consists of the secretions of the seminiferous tubules, epididymides, vasa deferentia, seminal vesicles, prostate, and Cowper's glands and the diffuse glandular cells which are present in certain parts of the urethra. As shown in Table 9 there are great differences in the volume of semen and numbers of spermatozoa in the different classes of animals. When semen was centrifuged and the volume of packed cells determined, it was shown that approximately 15 per cent of fowl semen, by volume, is composed of spermatozoa. Bull semen contains about 10 per cent sperm by volume (Shaffner and Andrews, 1943).

Thousands of chemical determinations have been made on the semen of various species and on the secretions of the various parts of the genital system. One of the chief purposes of such determinations has been to

gain information which would lead to the development of suitable artificial media for sperm. This approach has been of value but has many limitations. As biochemists well know, the determination of elements and simple compounds tells very little about the organization of complex biological systems.

TABLE 9.—SOME QUANTITATIVE DATA ON SEMEN AND SPERMATOZOA*

Animal	Volume per ejaculate, in cubic centimeters	Sperm per cubic millimeter	Total sperm in ejaculate
Boar	200	100,000	20,000,000,000
Stallion	100	60,000	6,000,000,000
Bull	3–4†	800,000	3,000,000,000
Ram	0.8	1,000,000	800,000,000
Dog	7.0	5,000,000‡	35,000,000,000‡
Cock	0.6	3,000,000‡	1,800,000,000‡

* Adapted from Table 3, p. 36, *U.S. Dept. Agr. Cir.* 567.
† About 1 teaspoonful.
‡ Estimates.

Numerous studies have been made of the heads of spermatozoa which have been separated from the semen, washed, and the tails removed by centrifugation. It is known that the sperm heads contain the basic protein, protamine, and certain inorganic bases in combination with nucleic acids. It is likely that these basic proteins are similar to the composition of the genes themselves, and it is also likely that it will be many years before their structure and composition are understood.

The semen itself is chiefly water, the amount differing with species and the relative concentration of sperm per unit volume of semen. The amount of water varies from about 90 per cent in man to about 98 per cent in the dog.

One of the limiting factors in the survival of single cells, such as blood cells, sperm, or bacteria, is the osmotic pressure of the medium. It has long been known that this is remarkably constant in fluids such as blood and milk, and in recent years many studies of the osmotic pressure of semen have been made. The most common method of doing this is by measurement of the depression of the freezing point; the temperature at which semen freezes is compared to the freezing point of water. The average depression of bull semen is 0.609°C.; ram semen, 0.641°C.; stallion semen, 0.595°C.; boar semen, 0.616°C.; and rabbit semen, 0.574°C. (Anderson, 1945). By the use of such methods Salisbury *et al.* (1948) have shown that the osmotic pressure of fresh, normal bull semen

is similar to that of cattle blood and that the formula of the sodium citrate buffer which would be isotonic with blood is different from that which has been widely used in the preparation of yolk-citrate dilutor for semen. To be isotonic with blood, heated sodium citrate solutions should contain 2.9 g. $Na_3C_6H_5O_7.2H_2O$ per 100 ml. of glass distilled water. The actual preparation of this dilutor will be discussed in a subsequent chapter.

The determination of the pH and buffering capacity of semen has been

TABLE 10.—CHEMICAL COMPOSITION OF NORMAL HUMAN SEMEN, PROSTATIC FLUID, AND SEMINAL VESICLE SECRETION*

	Semen				Prostatic fluid				Seminal vesicle fluid			
	No.	High	Low	Av.	No.	High	Low	Av.	No.	High	Low	Av.
	Per liter of fluid											
pH	9	7.36	6.9	7.19	3	6.6	6.33	6.45	2	7.32	7.26	7.29
Water, g.	13	944	891	918	5	936	927	932	2	900	880	890
Sodium, mM	14	133	100	117	5	158	149	153	1	103		
Potassium, mM	12	27.4	17	22.9	6	61.4	28.7	48.3	2	21.2	14.3	17.8
Calcium, mM	3	7.15	5.3	6.22	3	32.7	28.7	30.2				
Total CO_2, mM	7	33.2	19.2	24	3	5.4	3.1	4.2				
Chloride, mM	31	57.3	28.3	42.8	8	46.1	34.8	38.1				
Acid soluble phosphorus†	8	32.3	17.2	23.8	16	1.77	0.65	1.09	7	19.8	9.65	14.7
Specific gravity	6	1039	1031	1035	14	1027	1018	1022	2	1038	1036	1037
	Per 100 cc. of fluid											
Total nitrogen, mg.	34	1225	560	913	14	511	295	416	3	1343	1233	1284
Nonprotein nitrogen, mg.	12	130	73	96	6	90	30	53.6	1	....	....	99
Total protein by difference, g.	12	6.85	3.29	4.50	6	2.93	1.66	2.17	1	....	....	7.78
Total protein, gravimetric, g.	11	7.74	4.30	5.80	2	2.64	2.46	2.55	1	....	....	9.04
Globulins, g.	6	2.43	0.76	1.20								
Glucose,† mg.	6	369	203	295	12	48	Trace	16.4	5	625	275	390
Ascorbic acid,‡ mg.	9	....	....	12.8	19	....	....	0.54	9	....	....	4.66
Inorganic phosphorus,§ mg.	..	....	....	45								
Spermine phosphorus,§ mg.	..	....	....	22.5								
Urea,§ mg.	..	....	....	72								
Lactic acid,§ mg.	..	....	....	95								
Cholesterol,§ mg.	..	....	....	80	..	618	86‖					

* Huggins, C., Scott, W. W., and Heinen, J. H., 1942.
† Data of Huggins and Johnson (1933).
‡ Data of Berg, Huggins, and Johnson (1941).
§ Data of Goldblatt (1935).
‖ Data of Moore, Miller, and McLellan (1941).

used routinely in semen investigations. The pH of semen is affected by a wide variety of factors such as species, temperature, age of semen, relative amounts of fluid from the different accessory glands, frequency of service, season of the year, and numerous others. In farm animals the

pH is seldom less than 6 or more than 8 and tends to be confined to a narrow range around 7. The average pH of bull semen during a calendar year was 6.87 and was 7.04 for fowl semen during a similar period (Indiana Station). Smith and Asdell (1940) showed that bull semen is well buffered in the pH range 4 to 5.5 and 9 to 10, but relatively poorly buffered between pH 6 and 9.

The most common inorganic constituents of semen are sodium, potassium, calcium, magnesium, phosphorous, and chlorides. The actual amounts vary widely with species and the amounts of secretion from the various accessory glands. For detailed analyses in the boar the reader is referred to McKenzie, Miller, and Baugess.

Because of the importance of glucose and lactic acid in ordinary cellular metabolism, these organic constituents of semen have received the most attention. The wide range in these compounds reported by most investigators suggests that they may be influenced by many factors. One of the most recent studies of ram semen showed that the glucose content of 26 samples from 7 rams was 516.3 mg. per cent at the time of ejaculation with a standard deviation of 138.4 and a coefficient of variation of 26.8 per cent. The lactic acid content of fresh semen was 120 mg. per cent (Moore and Mayer, 1941). As summarized by Anderson (1945), bull semen has been reported to contain 100 to 495 mg. per cent glucose and 40 to 75 mg. per cent lactic acid and stallion semen, 0 to 116 mg. per cent glucose and 4.6 to 71.5 mg. per cent lactic acid. The production of acid from glucose or other substrates occurs rapidly in semen following ejaculation. This process is called glycolysis and is apparently due to the action of cell enzymes. At 0°C. glycolysis is practically absent, but goes on rapidly at body temperature. Although there is a correlation between rate of glycolysis and sperm motility, this method of evaluating the actual fertility of semen has not yet been of practical importance.

Semen has been reported to contain from 1.26 to 6.8 g. of total protein per 100 ml., depending on the species. In the human the greater part of the seminal proteins are proteoses. About 60 per cent of the proteins can be dialyzed through cellulose membranes impermeable to blood serum proteins. About 30 per cent of the total protein in human semen is globulin. Huggins *et al.* (1942) reported that in the human, semen protein is decreased by frequent ejaculation and subnormal male hormone production.

Anatomy of the Spermatozoa.—Spermatozoa were first observed by Ham, a student of Leeuwenhoek, in 1677, but their significance in inheritance was not realized at that time. About the middle of the eighteenth century, Spallanzani, by filtering semen, showed that the spermatozoa were the essential factor in reproduction, for the filtrate

proved to be impotent. Shortly after Kölliker had shown that the spermatozoa arise from the testes, Barry, in 1843, observed the conjugation of the sperm and egg in the rabbit.

The size of spermatozoa varies considerably in various animals but in any case they are extremely minute, that of the human being 1/300 in. in length. Savage and his coworkers state the head length of spermatozoa of the bull to be 9.7 μ and those of the stallion 6.16 μ. Phillips reports the head length of ram spermatozoa to be 8.15 μ. After puberty, spermatozoa are being continually produced in the testicles of the higher mammals at varying rates, and those not ejaculated are resorbed.

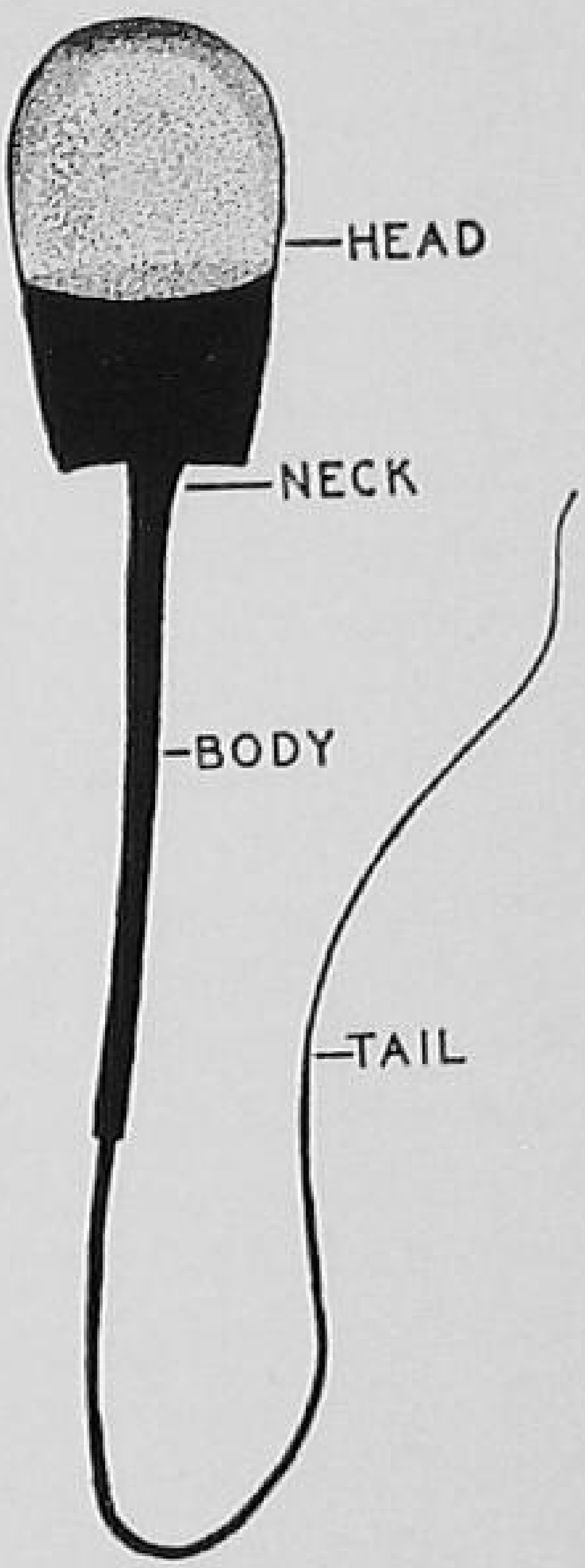


FIG. 37.—Generalized anatomy of the spermatozoon.

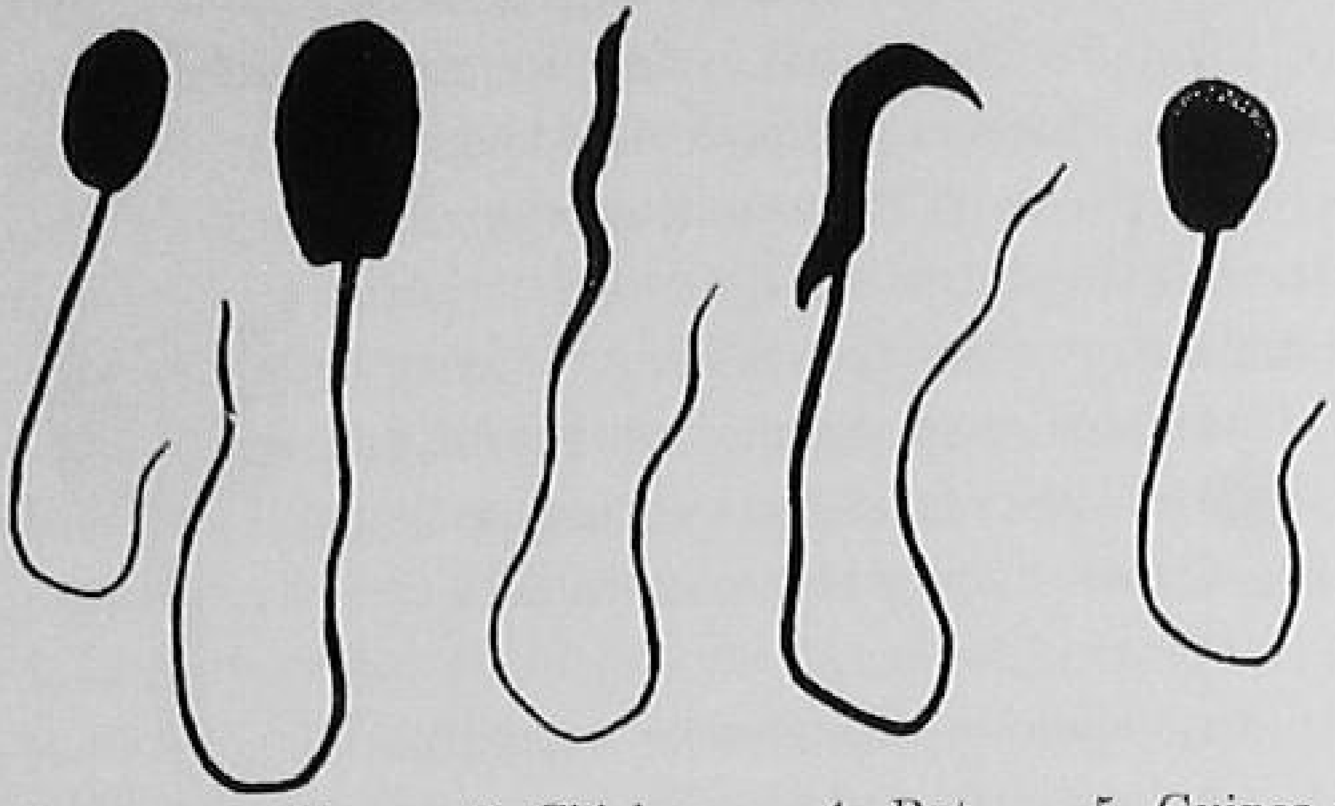
There are many species differences in sperm morphology. The general pattern in man and the farm mammals is very similar. Normal sperm consist of a head, neck, body, and a tail portion. The head, in profile, is flattened, but as ordinarily seen under the microscope is rounded or oval. It consists chiefly of nuclear material and is covered by a thin layer of cytoplasm. A caplike structure, the acrosome, is frequently observed on the anterior surface of the head. The head is of great importance because it contains the chromosomes.

The neck is very short and contains the anterior centrosome. The body is about the same length as the head. It contains the posterior centrosome at the neck end. A fibrillated filament extends from the posterior centrosome to the end of the tail. There are several sheaths around this filament in the body of the sperm. The tail is made up of two regions. The thicker portion is called the chief piece and the remainder, the end piece, is the bare continuation of the axial filament. The movement of the sperm is brought about by the lashing of the tail.

Physiology of the Spermatozoa.—Although spermatozoa are relatively simple cells morphologically, much is yet to be learned about their physiology.

The function of the spermatozoa is the fertilization of the ovum. The process of fertilization ordinarily takes place in several distinct steps: (1) insemination, the deposition of the sperm in the female genitalia, (2) the movement or transport of the spermatozoa to the Fallopian tubes,

(3) the penetration of the cell wall of the ovum by a spermatozoon, (4) the loss of the body and tail piece of the sperm, and (5) the union of the male and female pronuclei. The process of fertilization is not complete until the pronuclei of each gamete have united and the species number of



1. Human. 2. Sheep. 3. Chicken. 4. Rat. 5. Guinea pig.

FIG. 38.—Species differences in spermatozoa.

FIG. 39.—Normal bull sperm. Magnification approximately 200×.

chromosomes has been restored. It is generally said that a sperm has two functions, *viz.*, to contribute the paternal set of chromosomes and to initiate cell division on the part of the ovum. It has long been known that in some of the lower organisms, cell division can be mechanically induced. In this case the egg develops parthenogenetically and exhibits

only the maternal characteristics. Pincus and coworkers have been able to induce cell division and embryological development in the rabbit by altering the environment of the rabbit ovum.

Sperm Motility.—The most outstanding characteristic of spermatozoa is their ability to move. It is generally accepted that sperm which have lost their motility are incapable of fertilizing an ovum. The presence of motility, however, does not guarantee that the fertilizing capacity still exists. It is likewise well known that the more rapidly sperm move the shorter their length of life. Some of the basic problems in the preservation of semen for use in artificial insemination are the reduction of sperm motility during storage, the maintenance of the capacity for motility, and the reestablishment of vigorous activity after the sperm have been introduced into the female genitalia. It is not unusual for the motility of bull spermatozoa to persist for 3 weeks under laboratory conditions, but it is very unusual for conception to occur in cattle with semen which has been stored for 10 days. Shaffner (1942) was able to restore motility in fowl sperm which had been held at −79°C. for 14 months. Although motility was excellent, fertility was not induced.

Sperm Survival in the Female Genital Tract.—The fact that there are very great species differences in sperm survival in the female genitalia has resulted in many unsubstantiated beliefs concerning man and the farm animals. In most mammals it is very unlikely if sperm have a useful life of more than 36 to 48 hours. In fact, most animal-breeding specialists recommend that natural service or artificial insemination should precede the time of ovulation by only a few hours. In cattle, a species in which ovulation occurs about 14 hours after the end of estrus, the best results are obtained when service is given about 20 hours before ovulation occurs. In the chicken fertile eggs are commonly produced for 3 weeks following a single insemination and have been known to occur for as long as 32 days. Of the mammals, the bat seems to be in a special class. In some species of bats highly motile sperm have been found as long as 159 days following isolation from the male. Although, under natural conditions, bats may copulate during the winter and spring, it has been shown that sperm deposited in the fall are capable of fertilizing ova produced in the spring (Wimsatt, 1944). Among insects, the queen bee has been reported to lay fertile eggs for 7 years following the last insemination.

In spite of the above facts, we must realize that the store of energy in a tiny sperm is not overlarge and that, when the seminal fluid is deposited in the female genital tract of the higher animals, the spermatozoa are immediately plunged into violent activity. It would seem reasonable to expect, therefore, that their tenure of life would be brief. This

undoubtedly is generally the case, and we are safe in assuming that we can reckon their functional activity in hours rather than days. Because it has been shown also that the egg is generally capable of fertilization for a period of but a few hours following ovulation, it becomes obvious that the breeder's task is to see to it that viable sperm are deposited in the female genital tract at about the same time that the egg is released from the ovary.

Rate of Travel of Spermatozoa.—The older conceptions regarding the rate at which spermatozoa travel in the female genital tract were that it was a matter of several hours before they reached the distal end of the ovarian tubes. These ideas have had to undergo considerable revision in the light of later findings. When placed in proper media, mammalian spermatozoa have been clocked at speeds of from 1 to 4 or 5 mm. per minute with the average at about 3 mm. per minute. Many workers have found that the sperm reach the junction of the uterus and tube in periods as short as 10 minutes. As reviewed by Hartman (1939), Whitney (1927) recovered sperm in the ovarian bursa 18 minutes after coitus in the bitch, Lewis and Wright (1935) within 15 minutes in the mare, and Phillips and Andrews (1937) within 30 minutes in the ewe. More recent work in the ewe indicates that 20 minutes is sufficient for sperm to reach the upper portion of the Fallopian tubes (Schott and Phillips, 1941). Chicken sperm have been recovered in the upper part of the oviduct in 26 minutes (Mimura, 1939). Cattle sperm require as little as 2½ to 4 minutes to reach the oviduct (Van Demark and Moeller, 1950).

In some species it is possible for semen to be deposited directly into or through the cervix at the time of copulation. This is true of the horse and swine. However, even in the mare and sow, at least a portion of the semen is deposited in the vagina. The anatomy of the cow, ewe, and human is such that semen must be deposited in the vagina at copulation.

Transport of Spermatozoa in the Female Genitalia.—Many hypotheses have been proposed to account for the movement of sperm from the vagina to the distal ends of the Fallopian tubes. Since sperm are highly motile, they could move through the tract unaided. This is very unlikely. As previously discussed, in species in which the semen is deposited through the cervix, sperm should require less time to reach the Fallopian tubes. It has been suggested that muscular activity of the vagina and cervix at the time of copulation may be a factor and that at the time of the female orgasm the cervix may dilate and/or aspirate semen into the uterus. In some species copulation is followed by the development of a semen plug. The semen of the boar contains much coagulated material which could possibly act as a mechanical barrier pre-

venting the loss of sperm from the vagina. It is well known that the uterus undergoes rhythmic contractions and that the activity is usually greatest during estrus. It seems probable that uterine contractions are largely responsible for transporting sperm through the uterus and Fallopian tubes. Inert carbon particles, when mixed with semen, travel at approximately the same rate as sperm.

As previously mentioned, it is essential that sperm maintain the power of motility if fertility is to be preserved. It would appear logical to theorize that once sperm have been transported through the uterine horns and Fallopian tubes that they contact the ovum as the result of their swimming action and that contact with the ovum is maintained by the motile sperm.

The various means of evaluating semen quality, the dilution, preservation, and use of semen for artificial insemination will be discussed in another chapter.

Summary.—The male's part in reproduction consists of the production of spermatozoa and their deposition in the female genital tract at the proper time in relation to ovulation. The sperm are formed in the testis in the seminiferous tubules. They then pass through a series of small tubules into the epididymis where they undergo final maturation, and thence into the vas deferens where they are stored prior to ejaculation. The testis, in mammals, is ordinarily maintained in a rather vulnerable organ, the scrotum. This is essential if sperm are to be formed normally, since spermatogenesis cannot be completed in most mammals unless the testes are maintained at temperatures lower than those of the body cavity. In addition to the production of sperm the testis secretes the male sex hormone, testosterone, which is responsible for sex drive and the male secondary sexual characters. Male hormone and sperm production are usually synchronized, but may be independent under certain conditions. Testicular function depends primarily upon the gonadotropic hormones of the anterior pituitary gland. However, the maintenance of the male in a state of maximum reproductive efficiency requires a favorable environment, adequate nutrition, freedom from disease or physiological imbalance, and wise breeding management.

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CHAPTER V

THE FEMALE'S PART IN REPRODUCTION

In all the higher species of animals, fertilization and embryonic development take place within the female genital tract Understanding the structure and physiological functions of these organs is a prime requisite for anyone who would succeed in the art of livestock breeding. Enormous financial losses are incurred annually by breeders because of the difficulty so often experienced of getting females to conceive and, although it is unjust to lay all the blame at the door of the females, their share of the total fault is no doubt considerable. "Knowledge is power," and an understanding of the processes involved in fertilization, gestation, parturition, and lactation would often enable a breeder to avoid the fatalities that so often threaten individuals before as well as after birth.

Ovaries.—Mammalian females possess two ovaries, homologous to the testicles of the male; and, like the latter, the ovaries arise from the intermediate portion of the mesodermal somites and have a double function: (1) the production of ova or eggs and (2) the secretion of hormones. In other words, the ovary performs an ovogenetic as well as an endocrine function. The ovaries are generally spoken of as the primary organs of reproduction in the female because of their ovogenetic function and because they are the source of the female sex hormones. The development and functional activity of the remaining portions of the female genitalia are dependent upon the second function of the ovary, *viz.*, its endocrine function. An internal secretion of the ovary stimulates the growth of the uterus and vagina and other hormonal secretions from the corpus luteum, which appears cyclically in the ovary, sensitizes the uterine wall for the reception of the fertilized egg, maintains the pregnancy, and assists at parturition. These secretions together with others from the placenta and anterior pituitary stimulate mammary development and lactation following parturition. In some species ovogenesis is practically continuous after puberty. In others it occurs once, twice, or a few times a year.

In the higher animals, these glands are situated in the abdominal or the pelvic cavity suspended in the broad ligament. Their position varies somewhat in different species and in different individuals. They are attached to the broad ligament on one side at the so-called "hilum."

From this point the tissues of the broad ligament spread out and pass through the ovary, forming the ovarian stroma, made up of fibrous connective tissue. Toward the surface, the stroma becomes interspersed with glandular tissue that forms the ovarian cortex. Surrounding the ovary is a rather dense layer of fibrous tissue called the *tunica albuginea* and outside this is found a modified peritoneum, the inner portion of which consists of a single layer of cuboidal cells and which is known as the *germinal epithelium*. It is from the latter that the ova arise.

In the mare, the ovaries are somewhat bean-shaped and 2 to 4 in. in the longest diameter; in the cow, 1 to 1½ in.; in the ewe, ½ to 1 in.; and in the sow, somewhat larger than in the ewe and more irregular, owing

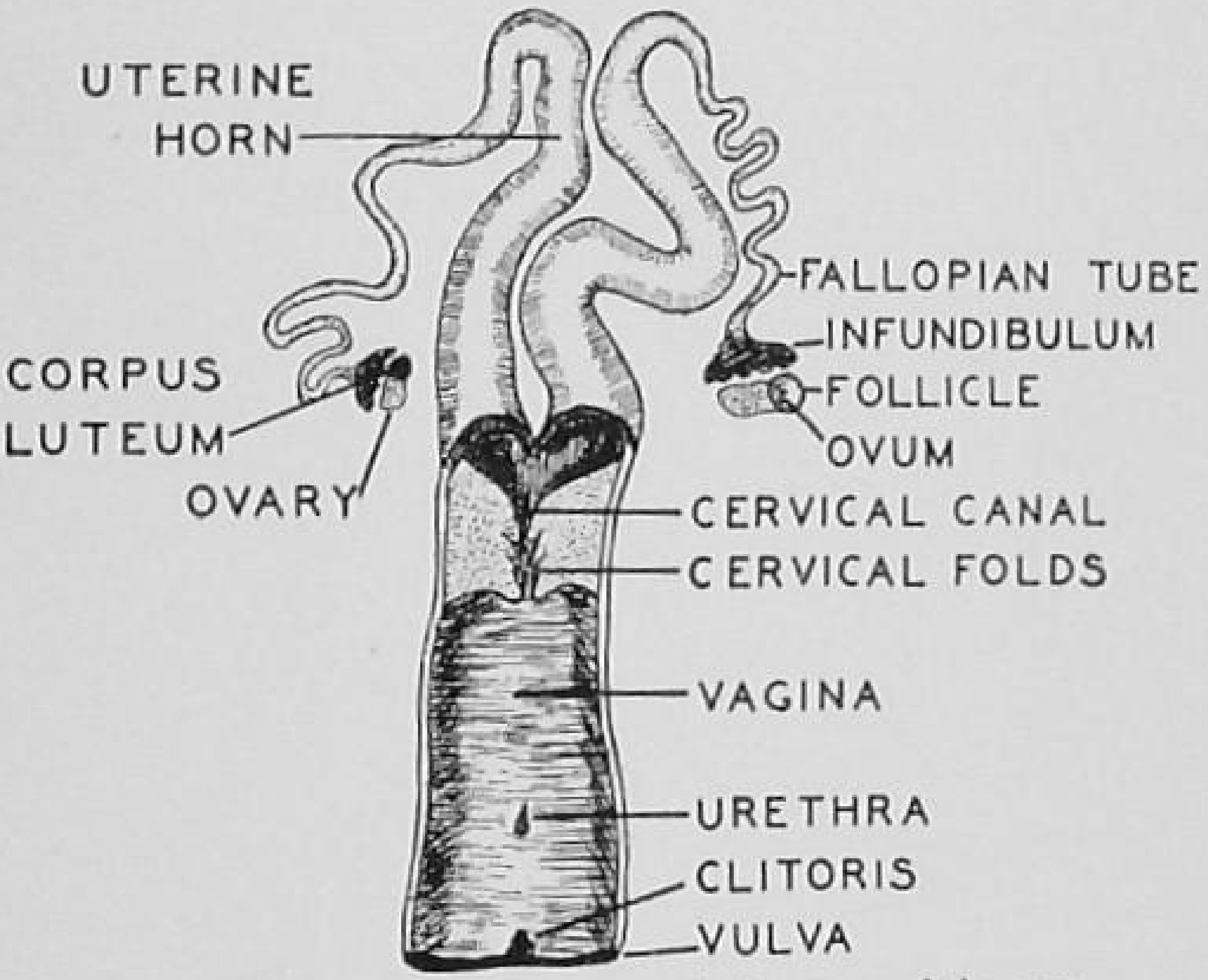

Fig. 40.—Diagram of the genital organs of the cow.

to the many protuberances of the follicles and corpora lutea which give them a shape somewhat like a bunch of grapes.

In the domestic fowl, and other avian species, only the left ovary is functional. During early embryonic life there are two female gonads, but the right remains as a functionless rudiment. During the egg-producing period the right ovary contains clusters of yellow or reddish-yellow spheres. These vary in size from the fully developed yolk to microscopic ova. Although they differ from mammalian ova in that they contain a large amount of yolk, they serve the same general function. It is interesting to observe that the chicken, the most highly developed of the farm animals from the reproductive standpoint, has only one functional ovary.

The ovary consists of glandular, connective, and nerve tissues, blood and lymph vessels, and many thousands of follicles in various stages of

development. The last, which arise from the germinal epithelium, are found all through the stroma of the ovary, and each contains an immature ovum that, when matured, is liberated and may be fertilized by a spermatozoon and produce a new individual. It has been estimated that there are upward of 75,000 follicles in the ovaries of a heifer calf at birth. Only a very small percentage of these follicles would ever ripen, even though

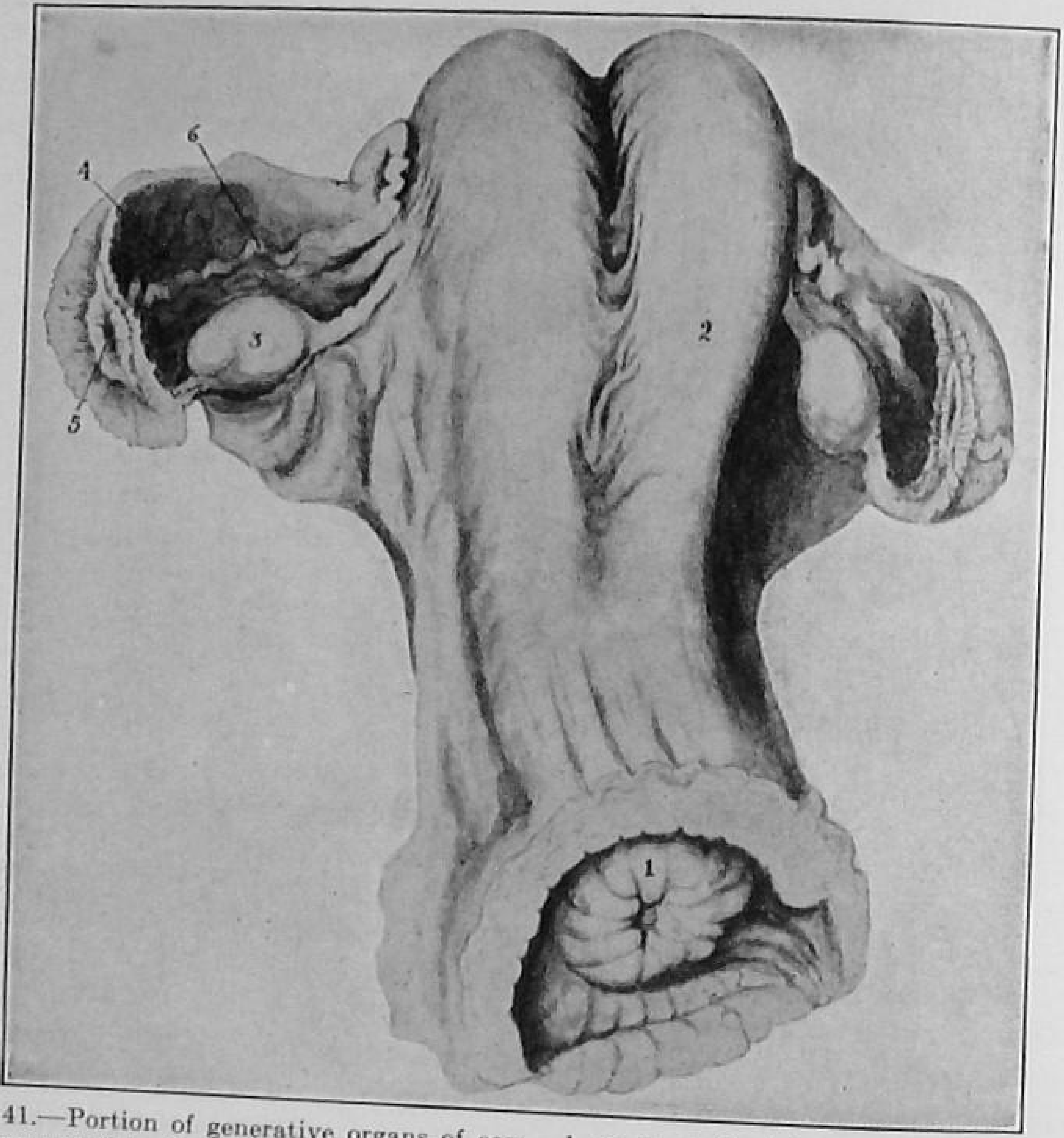

Fig. 41.—Portion of generative organs of cow. 1, os uteri; 2, right cornu; 3, ovary; 4, ovarian ventricle; 5, fimbriated end of oviduct; 6, oviduct. (*From Williams, Diseases of the Genital Organs of Domestic Animals.*)

the cow was never bred and came in heat regularly once in 3 weeks for 10 to 15 years. In this case, the ovaries would gradually become fibrous because of the deposition of the small plugs of connective tissue, the end result of the absorption of corpora lutea. The newer concept of a continual production of new ova from the germinal epithelium, similar to spermatogenesis in the male, would involve the production of even greater numbers of follicles, most of which atrophy and are absorbed

before reaching maturity. This continuous process of ovogenesis from the layer of germinal epithelium is comparable to the continuous process of spermatogenesis in the male. It is now claimed to exist in the mouse, rat, guinea pig, dog, cat, monkey, and mare, and is probably the general method of egg production of all the mammals. In either case, nature has attempted to ensure the perpetuation of the race by providing a superabundance of both spermatozoa and ova.

The ovarian follicle at the beginning consists of the egg cell surrounded by a single layer of epithelial cells Surrounding this is a specialized layer of ovarian connective-tissue stroma known as the *theca.*

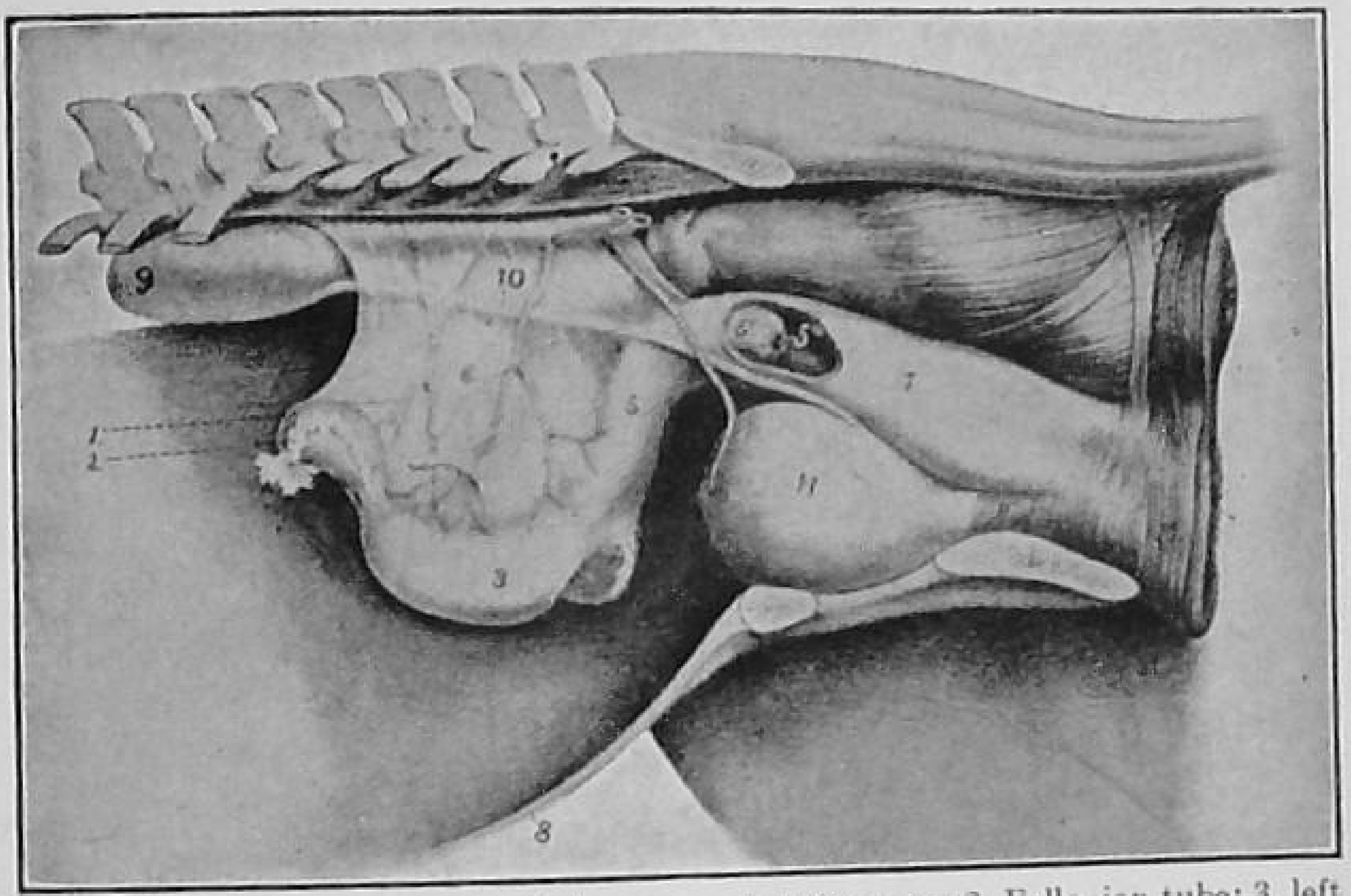

Fig. 42.—The generative organs of the mare. 1, left ovary; 2, Fallopian tube; 3, left horn of uterus; 4, right horn of uterus; 5, body of uterus; 6, broad ligament; 7, vagina; 8, abdominal wall; 9, left kidney; 10, left ureter; 11, urinary bladder. (*From Leisering, Atlas of the Anatomy of Domesticated Animals.*)

As growth proceeds, the epithelial cells multiply and push out away from the ovum forming an antrum, which becomes filled with a yellowish, alkaline, albuminous fluid, the liquor folliculi The ovum itself remains on a small hillock of epithelial cells, the cumulus oöphorus. There is some variation in the size of the ova of different mammalian species, but they measure on the average about 0.13 mm. This is greatly in excess of the size of the sperm, which has little or no cytoplasm. The egg, on the other hand, has a nucleus with its contained chromosomes of about the same size as the head of the sperm, and in addition it has a considerable amount of stored cytoplasm, or yolk, in which the nucleus is suspended. This makes the egg several thousand times the size of the sperm, but the dam is actually no more important than the sire from a hereditary standpoint, for both egg and sperm have a nucleus of equal size in which

are found an identical number of chromosomes (with the possible exception of sex chromosomes in some species). The stored yolk of the egg is presumably designed to provide energy for the developing zygote for the first few days following fertilization and until the zygote can pass down the ovarian tubes into the uterus and find another source of energy and materials for growth. The developing follicle passes toward the periphery of the ovary, finally protruding from the ovary to the extent of half its size or more preparatory to being liberated. This maturing of the ovum in the ovary occurs at more or less regular intervals in farm animals and is usually accompanied or preceded by estrus, or heat.

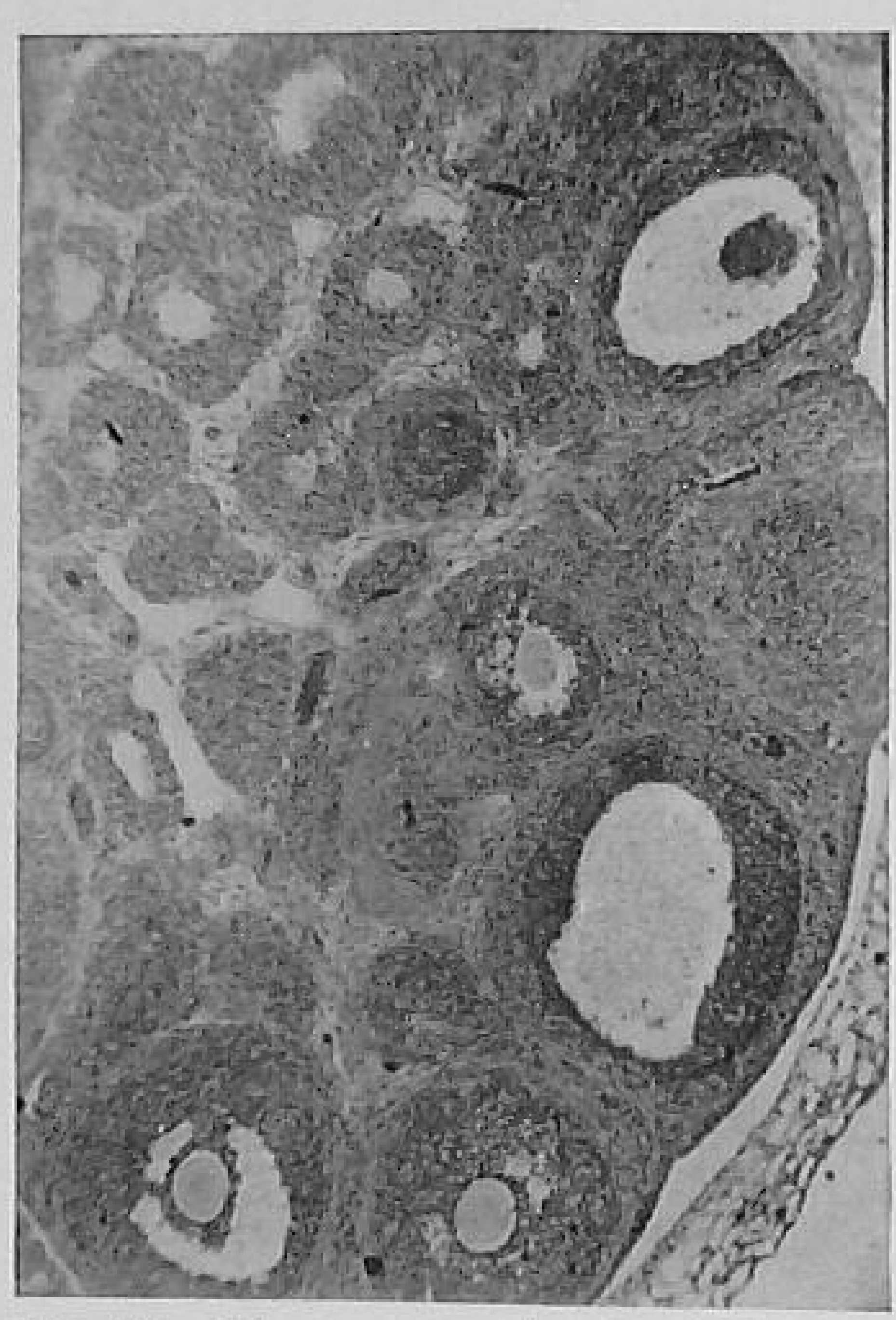

Fig. 43.—Mouse ovary showing follicles of different sizes and types.

This cyclic development of a mature ovum begins at puberty, under the stimulation of the anterior pituitary hormones. As noted in the previous chapter, the development of ova from Pflügers egg cords begins early in embryonic life. These embryonic follicles, however, and those from birth to puberty usually become atretic. Puberty marks the time when a follicle succeeds in reaching full maturity with the attendant maturing of the egg and reduction of the number of chromosomes to one-half. It is now thought that waves of follicles start developing cyclically throughout the reproductive life of the female, one or a few of them reaching full maturity, the others being resorbed preceding the next wave.

In the production of a functional ovum, or egg, the primordial egg cell in the follicle goes through two rapid cell divisions. Previous to the first division, synapsis occurs; and the net result of the first division, which takes place in the ovary in mammals, except perhaps in the bitch, is a reduction in the number of chromosomes to one-half the number characteristic of the species and the very unequal division of the cytoplasm. This is known as the *heterotypic division* and is followed by a second homotypic cell division in which the chromosome number is not further reduced. The one mature ovum now passes into the peritoneal cavity of the broad ligament and then into the uterine tube.

Starting with a primary germ cell, or oöcyte, in the ovary, the reduction

division, including synapsis, and the formation of tetrads is the same as found in the male, except that in the female, instead of two secondary spermatocytes, there are formed one secondary oöcyte and one non-functional polar body, each of which, however, has received one-half the

FIG. 44.—Maturation in ova of gonadotropin-stimulated mouse ovaries. Observe the chromosomes and the maturation spindles in the metaphase stage. Magnification approximately 1200×.

chromatin material and contains one-half the normal number of chromosomes. In effect, the nucleus, rather than the whole cell, divides. The polar body differs from the secondary oöcyte in having received none of the yolk or cytoplasm. These two, the secondary oöcyte and the polar body, then divide, the oöcyte giving rise to one ovum or egg and one more polar body. The first polar body may give rise to two polar bodies. The ovum is the female gamete that is capable of being fertilized

by a spermatozoon. The three polar bodies are nonfunctional and are later absorbed. So, whereas in the male there are produced four functional spermatozoa from each primary spermatocyte, from the primary oöcyte of the female in the higher forms there arises but one functional ovum and two or three nonfunctional polar bodies.

The purpose of the reduction division in the formation of germ cells, in both the male and the female, is to keep the number of chromosomes for the species constant. When an ovum with one-half the normal number of chromosomes is fertilized by a spermatozoon, also with one-half the normal number of chromosomes, the summation of the two halves restores the normal number of chromosomes in the zygote that is to produce the new individual. No doubt, some cases of sterility in hybrids are due to the fact that the two species that were crossed had different characteristic numbers of chromosomes, and, although fertilization and subsequent development are possible, it is nevertheless impossible for the hybrids to produce functional spermatozoa or ova, because the normal pairing of chromosomes and subsequent cell mechanism is interfered with.

So far as known, the distribution of chromosomes in germinal mitosis is at random. The solid chromosomes in Fig. 45 represent those contributed by the male, those in outline by the female. Following synapsis and disjunction, one member of each pair will proceed to one pole and be found in one cell, the other member of each pair will go to the other pole and be found in the other cell. The fact that one member of a certain pair goes to one cell has no influence on the distribution of any of the other chromosome pairs; in other words, the distribution is independent, or random, it being understood that one or the other member of each pair must normally go to each daughter cell. Figure 89 represents all the possible combinations of the eight chromosomes of Drosophila. As will be pointed out later, random distribution is one of the most potent causes of variation.

We meet here again the all-important fact that any of the higher organisms passes on to each of its offspring a sample half of its entire inheritance, one member of each pair of its chromosomes. Our whole purpose in making a study of breeding principles will be to learn how our animals may be made more pure in their genetic content of desirable genes, so that it will make no particular difference which member of each pair of chromosomes any offspring may chance to get.

Hormonal Regulation of the Ovary.—The normal development and function of the ovaries and the testes are dependent upon the gonadotropic hormones of the anterior pituitary gland. If these hormones are not secreted in proper balance in the mature female, the heat periods

may be irregular and normal follicular development and ovulation may not occur. As previously explained, there are two anterior pituitary gonadotropins. The follicle-stimulating hormone (FSH) is concerned primarily with the growth of the follicle. The luteinizing hormone (LH)

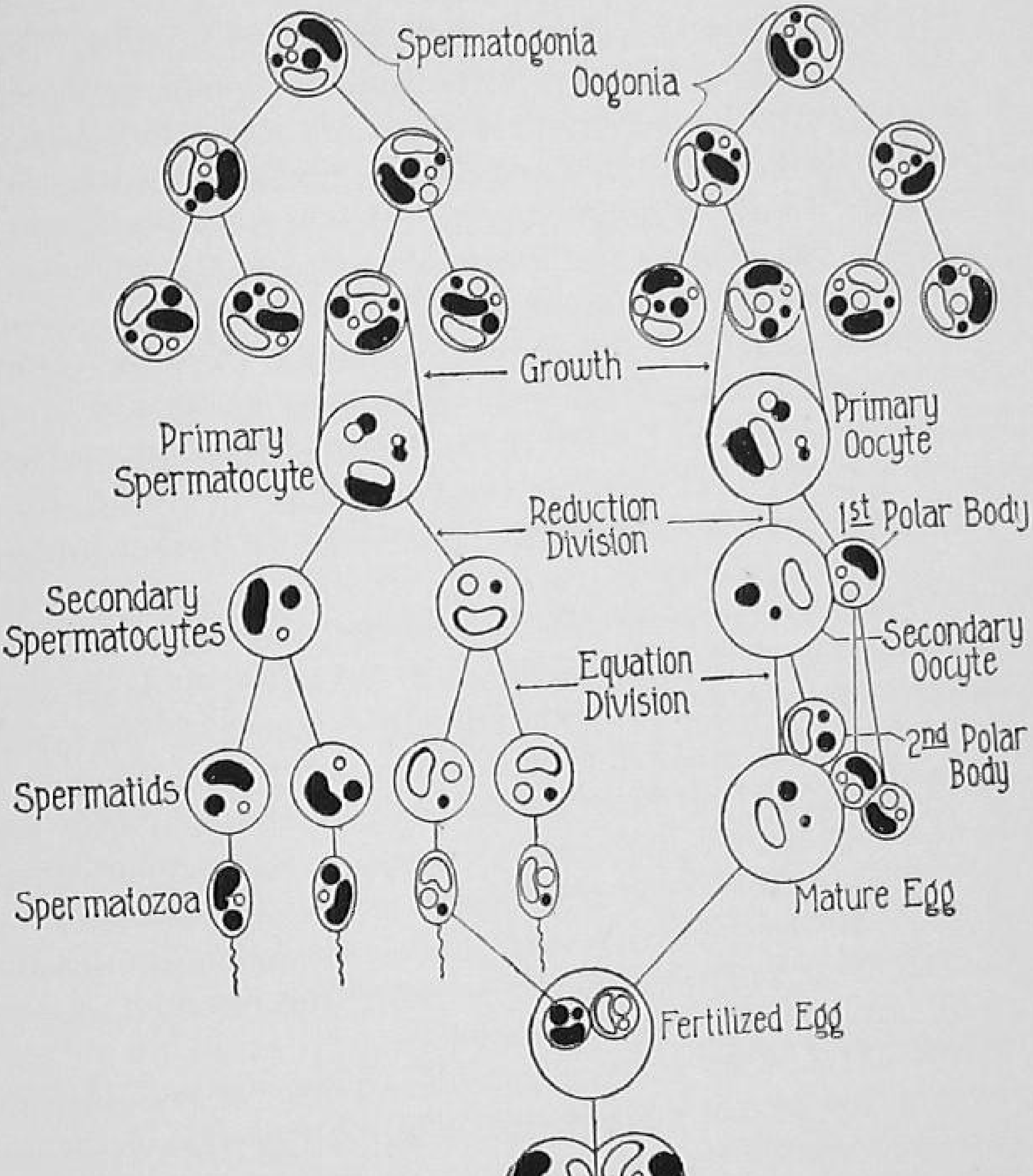

FIG. 45.—Diagram of maturation or miosis of germ cells in animals. The process begins with the third row of cells. Maternal chromosomes white, paternal black. All chromosomes in the fertilized egg received from the mature egg are thereafter maternal, and those received from the spermatozoon are thereafter paternal, regardless of what they were in the mature germ cells. (*After Shull.*)

is chiefly responsible for ovulation or rupture of the mature follicle and the development of the corpus luteum. There is some disagreement in different research laboratories as to the exact time relationships which are involved, but there is reasonable agreement in regard to the basic principles of the mode of action of the gonadtropins in the female.

In the ovary of the sexually immature female there are hundreds of small follicles. These are formed both prior to birth and puberty and continue to be produced even after the surgical removal of the anterior pituitary gland. Accompanying or probably causing puberty, FSH is secreted by the anterior pituitary in increasing amounts. Under the influence of this hormone a follicle, or follicles, grows rapidly. As the follicle grows under the influence of FSH, the anterior pituitary secretes minute but gradually increasing amounts of the luteinizing hormone. The LH causes the follicle to produce estrogen, the female sex hormone, and the female comes in heat (estrus). The increased secretion of estrogen by the follicle results in decreased production of FSH by the pituitary and increased secretion of LH. When LH is present in the blood in sufficient amounts, it brings about rupture of the mature follicle and the development of the lutein cells which form the corpus luteum. As the corpus luteum forms, it secretes the hormone progesterone, which is concerned with the final preparation of the lining of the uterus for pregnancy. Progesterone also inhibits the secretion of the gonadotropic hormones by the anterior pituitary gland. If pregnancy is not established, the corpus luteum eventually loses its function, ceases to secrete progesterone, and FSH is again produced in increased amounts and a new ovarian cycle is begun. If pregnancy is established, the ovaries usually cease to produce new follicles and ova until after parturition. In many seasonal breeders there is only one ovarian cycle each year. In cattle, on the other hand, the cycle is repeated at intervals of 19 to 21 days throughout reproductive life, unless pregnancy interferes. In summary, follicular development, estrus, and ovulation depend upon the interaction of the gonadatropic hormones FSH and LH and the two ovarian hormones estrogen and progesterone.

The Sexual Cycle.—The outstanding characteristic of the reproductive process in the female is its rhythmicity. All of the vertebrates which have been studied have definite reproductive cycles. There are wide species differences in the cycles, but each species has some basic pattern.

In most mammals the cycle is called the estrous or estrual cycle. Some animals, such as the fox, have only one heat period each year, and are called monestrous. The farm animals all have more than one cycle per year and are called polyestrous. Females, such as the ewe, which have a limited reproductive period are called seasonal breeders in contrast to the cow which is a continuous breeder. The estrous cycle can be divided into several distinct phases. The most easily recognized phase is the period of sexual receptivity, or heat, and is technically known as estrus. The stage following estrus is called metestrus. It is during

this period that the corpus luteum forms and secretes progesterone which brings about the final development of the uterus for pregnancy. If pregnancy does not occur, the corpus luteum regresses and there is a short period of genital rest called diestrus. Diestrus is followed by proestrus, which is characterized by follicular growth and generally heightened reproductive activity. Follicular growth is accompanied by the secretion of estrogen which gradually induces estrus. During heat the follicle usually reaches its maximum size, and ovulation occurs shortly before or just following the end of estrus. In seasonal breeders the genitalia have a long period of quiescence which is called anestrus. In cattle and swine the first part of lactation is usually accompanied by a period of sexual inactivity called lactational diestrus.

Table 11.—The Reproductive Cycle in Farm Animals

Species	Length of estrual cycle, days		Length of estrus		Usual time of ovulation	Length of gestation, days		Age at puberty, months
	Av.	Range	Av.	Range		Av.	Range	
Mare	21	10–37	5–6 days	1–37 days	24–48 hours before end of estrus	336	310–350	10–12
Sow	21	18–24	2–3 days	1–5 days	Usually second day of estrus	112	111–115	3–7
Ewe	16	14–20	30 hours	20–42 hours	1 hour before end of estrus	150	140–160	4–8
Goat	20	12–25	36–48 hours	20–80 hours	Near end of estrus	151	140–160	4–8
Cow	19–20	16–24	16–20 hours	8–30 hours	14 hours after end of estrus	281	274–291	4–8

Because small quantities of blood sometimes appear in the genital secretions of the cow and bitch, it is frequently said that menstruation occurs. This is not the case, and the terms menstruation and menstrual cycle should be reserved for the Primate. Menstruation is the shedding or elimination of a large portion of the uterine lining (endometrium) at regular intervals—usually each 26 to 30 days. In the Primate ovulation occurs at approximately the midpoint of the menstrual cycle. Thus ovulation would be most apt to occur 14 days after the beginning of menstruation in a female with a 28-day menstrual cycle. Primates, unlike other mammals, do not have a limited period of sexual receptivity and thus no outward manifestations which can be easily correlated with ovulation. The farm animals are characterized by the presence of a very limited period of estrus which is closely correlated with ovulation.

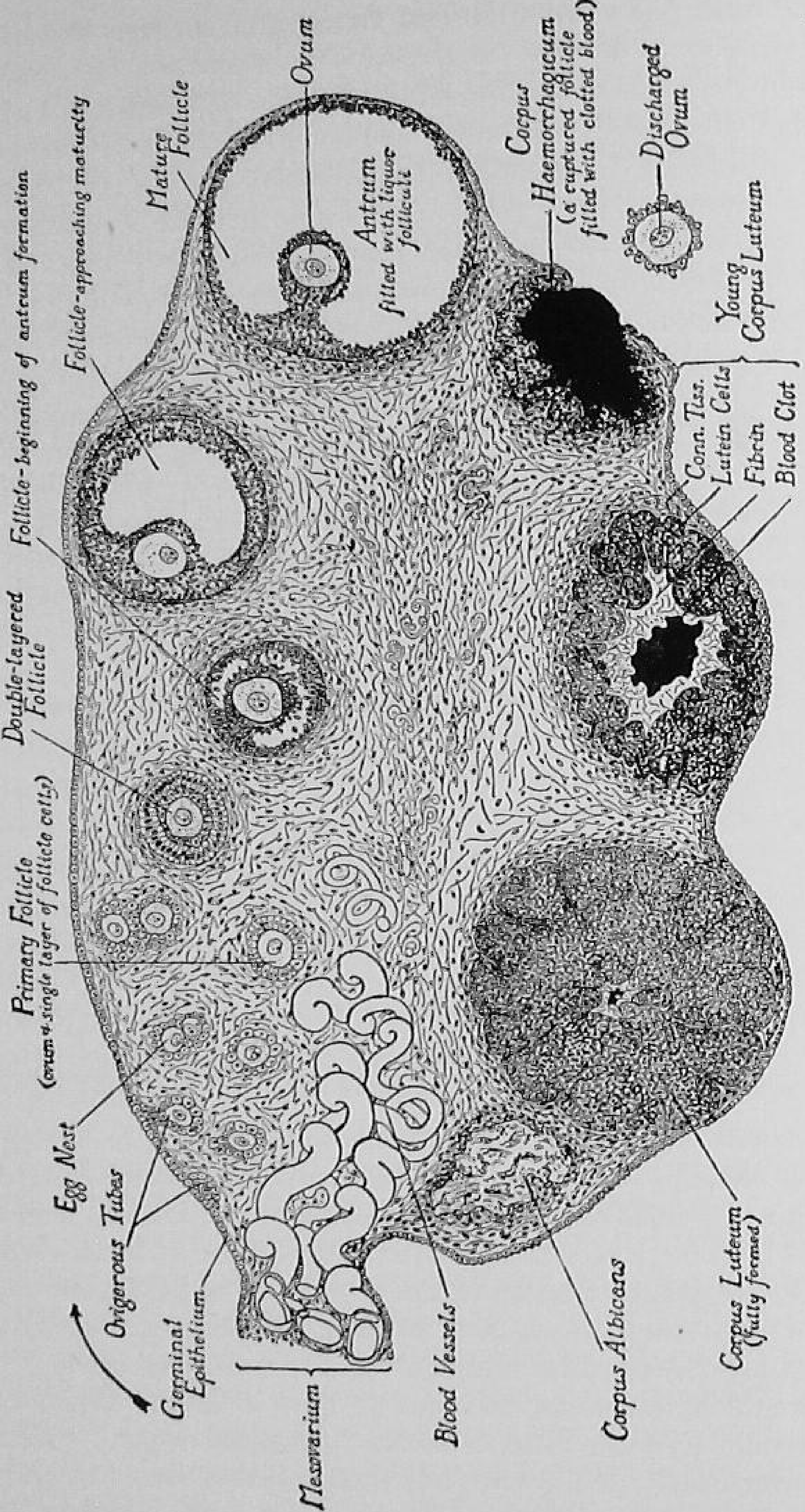

FIG. 46.—Schematic diagram of mammalian ovary showing the sequence of events in the origin, growth, and rupture of the ovarian (Graafian) follicle, and the formation and retrogression of the corpus luteum. Follow clockwise around the ovary starting at the arrow. (*From Patten, Embryology of the Pig, 2d ed., The Blakiston Company.*)

FACTORS INFLUENCING THE SEXUAL CYCLE

Age.—Sexual maturity is a gradual process. The appearance of heat does not necessarily mean that normal fertility has been attained. During the transitional period of puberty the sexual cycles may at first be irregular. Ovulation may occur in the absence of estrus, and estrus without ovulation is not uncommon. After full sexual maturity has been attained, the sexual cycles are usually regular throughout life. In the human, the reproductive processes usually cease in later life; this is called the menopause. In the farm animals old age itself is rarely the cause of reproductive failure. The age at puberty is approximately the same as previously given for the male. In sheep, however, the seasonal factor is important. Whereas sperm first appear in the ram at five or six months of age, sexual cycles are not initiated in the ewe until fall. Thus a lamb born in January would probably not exhibit sexual activity until September. There are, of course, wide species and individual variations in the time of puberty. Some of these will be discussed in the chapter on Reproductive Efficiency.

Seasonal Periodicity, the Breeding Season.—The effects of season on reproductive activity are more easily recognized in the female than in the male. As previously explained, this is sometimes due to the fact that some males may exhibit marked sex drive in the absence of spermatogenesis, *e.g.*, the ram. In seasonal-breeding females estrus is not manifest except during the breeding season.

Most of the wild mammals are monestrous. The dog and the cat usually have two estrual cycles annually. Sheep are polyestrous, but in the Northern Hemisphere the cycles are usually limited to the period between August 15 and January 30. Goats are very similar to sheep, the breeding season usually extending from September through December. Estrus occasionally occurs in sheep and goats in the spring and summer months, but planned breeding can rarely be expected during this period. Cattle, swine, and horses exhibit reproductive activity throughout the year but, as explained in the previous chapter, seasonal tendencies still persist. In the Western range states cattle breeding is largely a seasonal operation. Environmental and nutritional conditions are such that it is most satisfactory to have the calves born in the spring. For obvious reasons, the calving period is somewhat later in the Northern areas than in the South and Southwest. For very practical reasons swine breeding in the corn belt is seasonal in nature. When the two-litter system is used, the sows are bred to farrow in the spring and fall. The majority of swine men using the single-litter system farrow their sows in the spring. Thus, although both cattle and swine can reproduce

throughout the year, man has done much to keep them on a seasonal schedule. Mares, if well cared for, are capable of continuous reproductive activity. Animals which are not well fed, and some which are, are most apt to exhibit estrous behavior during the spring and summer months. When horse production was more important than at present, by far the greatest number of mares were mated in the spring and summer.

Light and Temperature.—The mode of action of light and temperature upon reproduction in the female is probably rather similar to that described in the male. The effects of light in stimulating fall and winter egg production in chickens are well known. Although the total annual egg production is increased but slightly, the hens are induced to lay in the fall and winter when the prices of eggs are highest. It seems clear that the effects of light are upon the anterior pituitary gland and its secretion of the gonadotropic hormones. In the chicken both egg production and fertility are lowest during the summer. It is difficult to separate the effects of light and temperature, but it has been hypothesized that decreased thyroid activity during the warm months may indirectly reduce reproductive efficiency. In human gynecology it is frequently reported that the correction of subnormal thyroid activity is followed by pregnancy. Although conclusive experimental proof of such hypotheses is lacking, they are worth consideration. Temperature, light, and humidity are very difficult to control in large-animal experimentation. Studies with goats by Bissonnette (1941) and by Sykes and Cole (1944) strongly suggest that increased light followed by decreased light, in an attempt to duplicate seasonal changes, will induce out-of-season breeding activity.

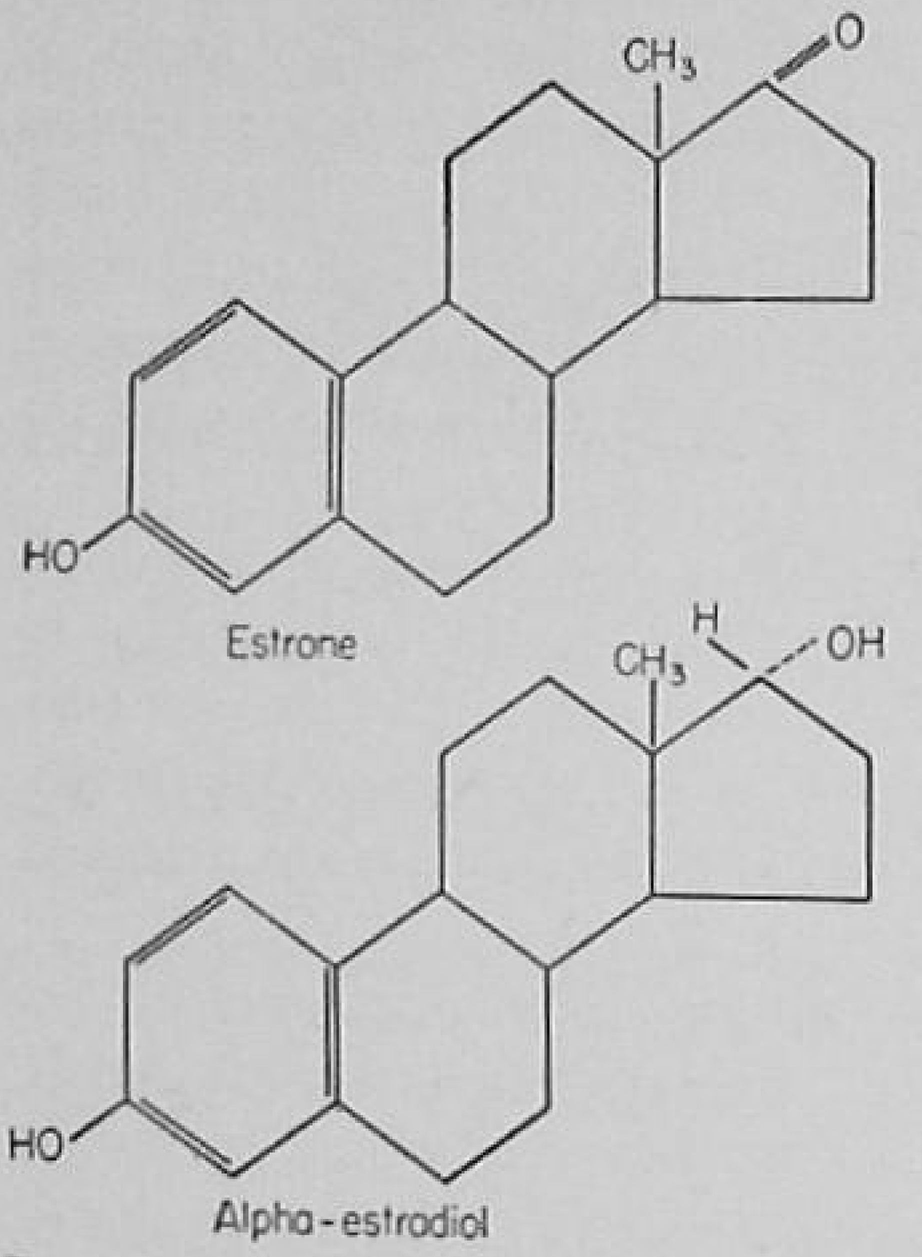

FIG. 47.—Structural formulas of two of the common female hormones.

The Hormonal Functions of the Ovary.—The endocrine activity of the testis is simple by comparison with the ovary. In the male the androgenic hormone is produced at a more or less continuous rate throughout the reproductive period. In strictly seasonal breeders, of course, the male hormone is produced in maximum amounts only during the breed-

ing season. The ovary produces at least two distinctly different hormones. These are produced only at definite times during the sexual cycle, and the levels of secretion of each hormone vary during the cycle.

Estrogen.—It has been known since the 1890's that atrophy of the uterus following castration could be prevented by an ovarian graft. Long and Evans (1922) and Allen (1922) suggested that the substance responsible for the maintenance of the uterus was produced by the Graafian follicle, and this was proved by Allen and Doisy in 1923. Many workers regard these studies as the beginning of modern endocrinology. The hormone produced by the Graafian follicle is commonly referred to as the female sex hormone and is one of a large number of the estrogenic hormones. During the early 1920's it was thought that this was the only ovarian hormone.

It is now known that at least 10 different estrogens appear in animal tissues, secretions, blood, or urine, and that many others with estrogenic activity can be prepared synthetically. Estrogens have been isolated from the ovary, placenta, testis, and adrenal cortex and from various plants. They are found in large amounts in the urine of both males and females and such unlikely sources as petroleum and the slime from the bottom of the Dead Sea.

The first estrogen to be crystallized and chemically identified was estrone. This hormone was isolated from the urine of pregnant women by Doisy *et al.* in 1929. The most active natural estrogen, and the one which is probably secreted by the Graafian follicle, is estradiol. It is very similar to estrone in structure but has considerably more physiologic activity.

The natural estrogens have little effect unless they are administered by injections, *e.g.*, subcutaneously or intramuscularly. During the 1930's many compounds which do not appear in nature but which have great estrogenic activity were synthesized. Many of these compounds are dissimilar chemically from the natural estrogens, and some are very effective when administered orally. One of the best known is diethylstilbestrol. It can be synthesized at low cost, is more active physiologically than most of the natural estrogens, is orally active, and has few undesirable side effects. Diethylstilbestrol is widely used in human and animal medicine for the correction of reproductive disorders. In addition to its effect on the genital system it has been shown to be capable of inducing fattening in chickens (Andrews and Bohren, 1947, and others) and of increasing growth in cattle and sheep (Dinnusson *et al.*, 1949, and Andrews *et al.*, 1949).

Progesterone.—The physiologic importance of the corpus luteum has

long been known, although the substance responsible for the effects was not isolated until 1934. Beard suggested in 1897 that this structure was necessary during pregnancy and would likewise affect ovulation and the estrous cycle (Turner, 1948). The general descriptive name of the corpus luteum hormone is *progestin* and the crystalline hormone itself is called *progesterone*. Progesterone is a steroid hormone closely related chemically to both the natural estrogens and androgens. It is produced cyclically during the estrous cycle, reaching a peak during the late metestrous stage of the cycle. It is secreted in large amounts during early pregnancy and can apparently be produced by both the corpus luteum and placenta.

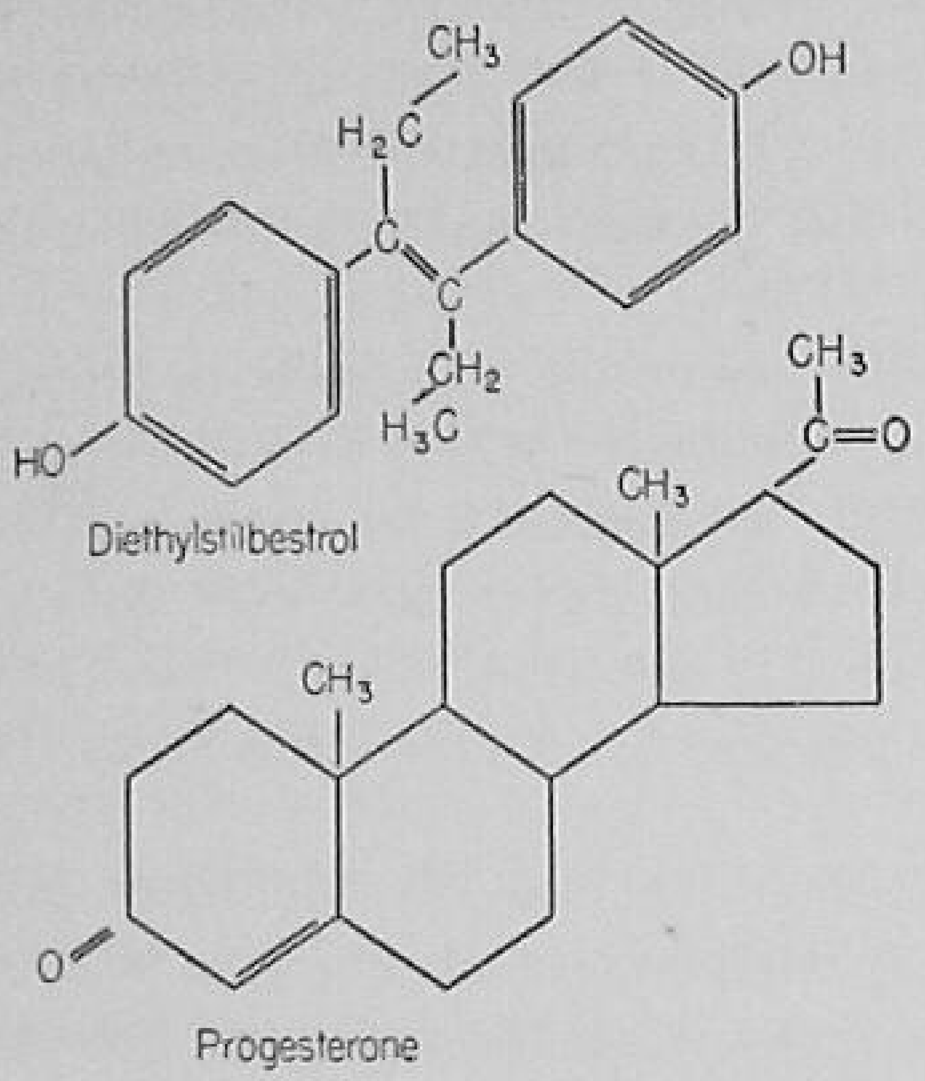

FIG. 48.—Structural formulas of diethylstilbestrol and progesterone.

Androgen.—It is clear that the ovary, in addition to secreting estrogen and progesterone, can produce significant quantities of androgen. Whether the ovary normally secretes androgen in small amounts is not known, but there is no doubt of its androgenicity under certain special conditions. When ovarian grafts have been made into the ears of castrate rats and mice, sufficient androgen has been produced to maintain the male accessory glands (Turner, 1948). The temperature of the graft site may be of some importance, since the ear has a lower temperature than the normal abdominal ovarian location.

Effects of the Ovarian Hormones on the Genital Organs.—The most easily recognized effect of the estrogens is their stimulatory action on the vagina. This effect is the basis of the most commonly used biologic test for estrogenic activity. Prepubertal castration of the rat or mouse prevents the development of the vagina. The opening of the vaginal canal is prevented or greatly delayed, and the vagina has only a very thin lining of epithelial cells. The injection of estrogen in such an animal causes precocious opening of the vagina and the development of a very thick lining of epithelial cells. These cells are produced in great quantities by the germinal epithelial layer. As new cells are produced, the innermost cells are sloughed off and appear as large scaly cells with indistinct nuclei. These cells can be obtained for study by introducing a swab into the vagina and making a smear on a glass slide for microscopic study. The presence of large numbers of such large scaly cells is indica-

tive of an estrogenic effect. This method is very accurate for the detection of minute quantities of estrogen and is widely used in biology and medicine. Likewise, the condition of the vaginal epithelium in normal animals is indicative of the stage of the estrual or menstrual cycle and has wide application in clinical studies.

The development of the uterus is dependent upon both estrogen and progesterone. Development is initiated by estrogen and completed by progesterone. Estrogen injection of the castrate is followed by increased proliferation and activity of the epithelial cells lining the uterus and of the smooth muscle cells of the myometrium. The activity of the uterine glands is ordinarily stimulated first by estrogen and is then continued by progesterone during the luteal phase of the cycle. Uterine activity, as measured by the rhythmic contractions of the uterus, is maximum during estrus, and the uterus is relatively quiescent when progesterone is being secreted by the corpus luteum.

As previously discussed, the corpus luteum is present and functional only at certain stages of the estrous cycle and during pregnancy. The primary function of its hormone, progesterone, is the final development of the uterine epithelium in preparation for implantation of the blastocyst. Progesterone is concerned with the maintenance of pregnancy following implantation. In the cow, removal of the corpus luteum from the ovary during pregnancy, especially during the first half of pregnancy, will nearly always result in abortion. In the mare, the ovaries may be removed during early pregnancy without causing abortion. This is assumed to indicate that the presence of a functional corpus luteum in the ovaries of pregnant animals is essential in some species and not in others. It is known that the placenta can produce progesterone, estrogen, and even gonadotropins, and this may explain some of the species differences in dependency on the ovaries during pregnancy.

The Ovarian Hormones and Secondary Sexual Characteristics.—Like the male, the female also exhibits characteristics peculiarly associated with her sex and referable, as are the development and functional activities of the accessories, to hormones secreted by the ovaries. This is one of the main functions of the ovaries.

These characteristics are to be found largely in the general body form and are generally not so striking as those found in the male. The typical male form is heavy or well developed anteriorly, less well developed posteriorly. In the female, the exact opposite prevails. The mammalian female develops a wider pelvis and a general feminine type expressed in finer bone and more refined features than the male. The deposition of fat differs from that in the male, the voice is higher pitched, and she differs also in psychological traits.

Miscellaneous Effects of the Ovarian Hormones.—The estrogens have very definite effects on the skeletal system. Although skeletal growth is dependent chiefly on the growth hormone of the anterior pituitary gland, both estrogen and androgen stimulate or inhibit growth, depending on the levels at which they are present. Precocious secretion of the sex hormones tends to bring about closure of the epiphyseal junctures of the long bones and skeletal growth stops. In the castrate, because of the removal of the sex-hormone influence, skeletal growth may continue beyond the normal limits. The injection of both estrogens and androgens at certain optimum levels has been shown to increase growth rate.

As will be discussed in a later chapter, the estrogens are concerned in the development of the mammary system. Numerous secondary effects have been attributed to the estrogens. Depending on the species and the type and level of estrogen administration, they have been reported to affect fat deposition, calcium metabolism, nervous activity, metabolic rate, blood-cell formation, vascular phenomena, and many other body activities.

Muscular activity of the uterus is greatest during the phase of maximum estrogen secretion. The injection of progesterone, or its secretion during the luteal phase of the estrual cycle, is followed by uterine quiescence. The reason for this sequence of events appears to be concerned with the transport of sperm in the female genitalia during estrus. The less motile stage would seem to be conducive to the implantation of the developing blastocyst. In humans with histories of habitual abortion, progesterone is frequently administered because of its depressing effects on uterine motility and its stimulatory action on endometrial growth. There are obviously many different causes of abortion, and progesterone could not be expected to have beneficial effects where some specific cause, such as brucellosis in cattle and swine, is present. Like estrogen, progesterone is concerned with development of the mammary glands.

Estrous Behavior.—It is frequently assumed that estrus, being the only phase of the estrous cycle which is easily recognizable, needs no further discussion. Since the widespread adoption of artifical insemination, it has become increasingly apparent that many livestock breeders cannot recognize estrus and do not appreciate its full significance. In the farm animals there is a definite relationship between estrus and ovulation. If service or artificial insemination is carried out in relation to a particular stage of estrus, breeding efficiency can usually be increased. Under natural conditions females probably mated several times during estrus, thus increasing the likelihood of fresh sperm being present in the uterus

at the time of ovulation. If mating occurs only once during heat, the time relationships are of vital importance.

In all the farm animals estrus or heat is recognized by the willingness of the female to accept the male. In the ewe and mare the usual outward signs are the fact that the female stands and will allow the male to mount. Mares react very vigorously when not in estrus and may severely injure the stallion. For this reason, it is recommended that mares be tried to a stallion in some sort of a teasing stall or chute. Sows may occasionally exhibit both male and female mating behavior, but the estrous animal is usually recognized by her willingness to accept the male. Of the farm animals, cows are most likely to exhibit both male and female mating behavior. This has led to numerous errors in artificial insemination associations, and the "wrong" cow has often been kept in the barn for the insemination. Ordinarily, the truly estrous cow is the one which is mounted by other cows. When one female is approached by several cows, there should be little doubt that she is in heat. Fortunately, there are some physiologic as well as behavioral signs of estrus. Estrus is usually characterized by increased genital secretion and discharge due to stimulation by the estrogenic hormone. In cattle and swine there is frequently some swelling of the vulva and urination may be frequent.

Following the discovery of estrogen, it was concluded that this hormone was solely responsible for estrous behavior. The experimental study of estrus indicated that androgens and progesterone, as well as estrogen, may be involved. In the spayed guinea pig sexual receptivity depends upon the secretion of estrogen followed by the secretion of small amounts of progesterone. In this species it has been shown that progesterone is secreted by the Graafian follicle prior to ovulation (Dempsey *et al.*, 1936). This has recently been shown to be true in the rat, mouse, and hamster (cited by Cole, 1948). Cole (1948) has found that in the ewe androgen, in combination with equine gonadotropin, was quite effective in inducing estrus. Since androgens are present in significant amounts in the female of several species, this reaction might not be limited to the ewe.

Ovulation.—Ovulation is the freeing of the ovum by the rupture of the follicle in the ovary. As indicated in the previous section, this takes place in animals during the estrus or heat period, except those, of course, which do not ovulate spontaneously. Many theories have been proposed to account for the freeing of the egg from its follicle; *e.g.*, pressure from within the follicle, pressure induced from the blood supply of the ovary, muscular contractions in the ovary or the follicle, and the action of proteolytic enzymes in the liquor folliculi.

Most animals, including all the farm animals, ovulate spontaneously. That is, ovulation does not depend upon copulation. The rabbit differs in that some type of stimulation, such as copulation, mechanical or electrical stimulation of the cervix, or other afferent stimuli, is necessary

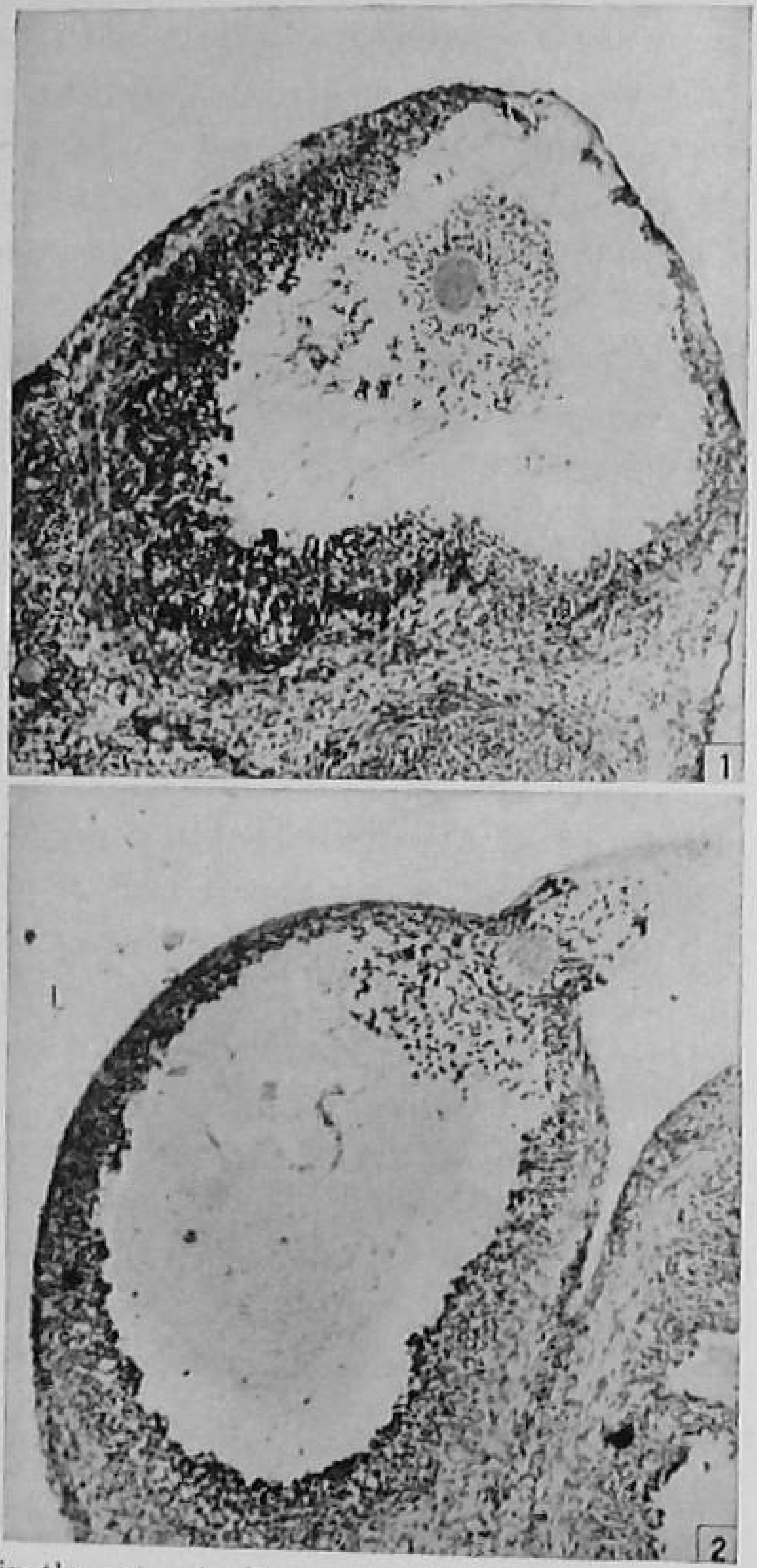

FIG. 49.—Ovulation in the rat. 1. Ovum detached from germinal hill and approaching stigma. 2. Rupture of the stigma and passage of the ovum through it. (*Courtesy of Dr. Richard J. Blandau, University of Washington, School of Medicine*).

if ovulation is to occur. In the species in which the mechanisms of ovulation have been studied, whether they ovulate spontaneously or are similar to the rabbit, it appears that the primary regulation is by hormones.

As previously mentioned, ovogenesis and follicular formation can proceed in a limited way in the absence of the gonadotropic hormones.

However, the gonadotropins are needed for the development of Graafian follicles and ovulation. The most rapid phase of follicular growth appears to occur under the influence of FSH. In experimental animals under the prolonged influence of FSH the follicles become large and cystic and do not rupture. In normal animals it is thought that as follicular growth proceeds the anterior pituitary gland secretes increased amounts of LH, and that ovulation occurs when a certain balance between FSH and LH is reached. In the rabbit, copulation stimulates the release of anterior pituitary gonadotropins apparently as the result of transmission of the stimulus to the pituitary through the nervous system.

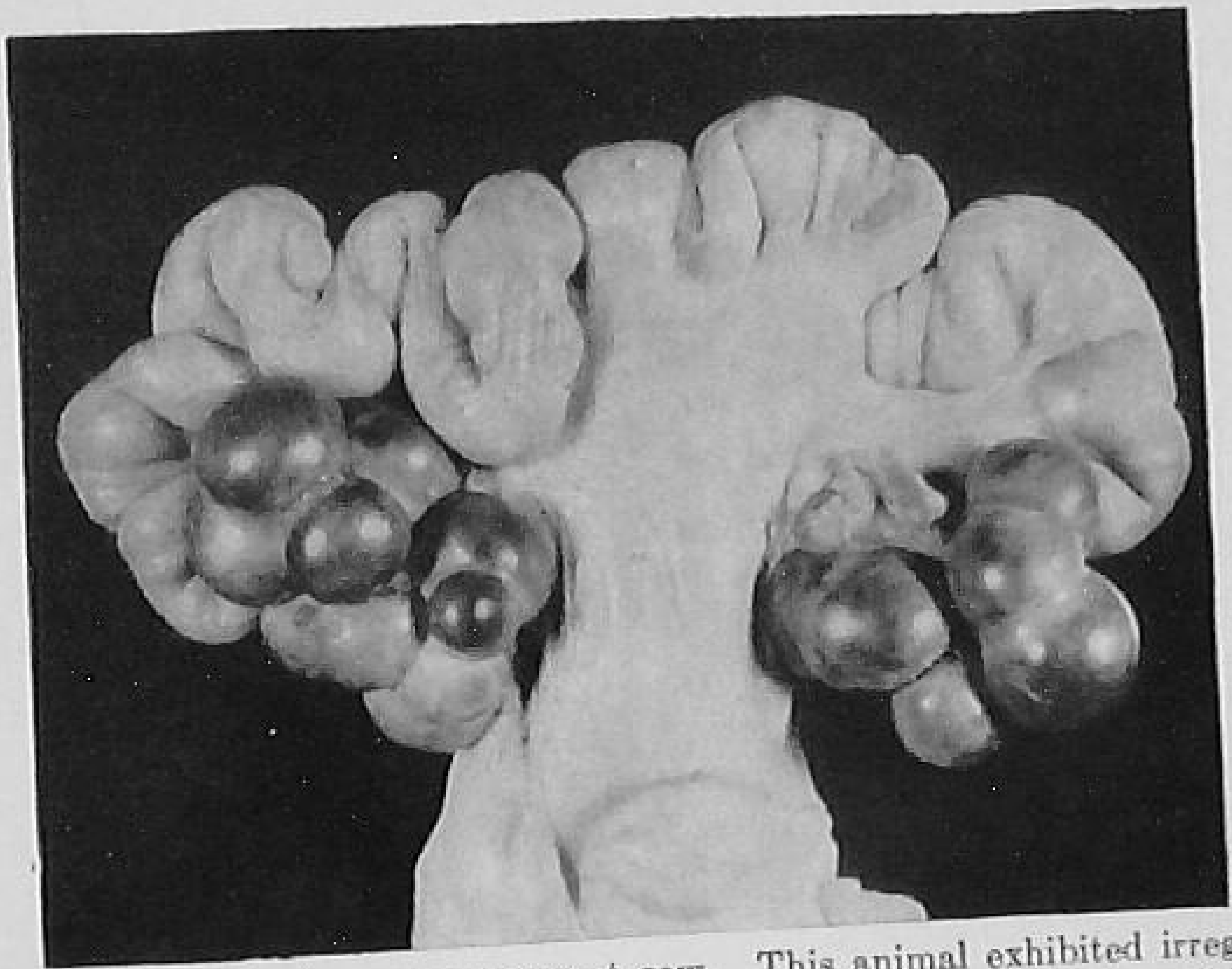

FIG. 50.—Cystic ovaries in a nonpregnant sow. This animal exhibited irregular estrual periods and had been bred repeatedly during a 5-month period without the establishment of pregnancy. (*Courtesy of Dr. A. V. Nalbandov, Department of Animal Science, University of Illinois.*)

The process of ovulation is a gradual one and not in any sense explosive or cataclysmic. The ripened follicle protrudes beyond the surface of the ovary, one or several areas of the follicular wall become avascularized, thin, and more or less transparent until the wall finally ruptures at one point. The follicular fluid flows through the ruptured area carrying the ovum with it.

During the final stages of follicular development the chromosomes in the egg are reduced to one-half the somatic number by the budding off of a polar body containing the chromosomes but little or no cytoplasm. As the time of ovulation approaches, the germinal hill (discus proligerus or cumulus oöphorus) breaks up, freeing the ovum in order that it will not be trapped in the follicle.

There have been many suggested schemes in regard to the alternation

of ovarian function. The theory that one ovary produces male and the other female offspring is obviously unworkable in mammals in view of what is known of the genetic determination of sex. There is no evidence to substantiate the idea that the ovaries alternate in egg production. Alternation sometimes occurs, but the usual pattern of ovarian activity is a random one. The removal of one ovary usually has little or no effect on subsequent fertility.

Breeding in Relation to Time of Ovulation.—The time of ovulation is of very great practical importance to livestock breeders. Relatively little was known about the time or process of ovulation before 1930, and in cattle the matter had received little attention prior to 1940. The "average" time of ovulation of the various classes of farm animals is known, but as in all biological phenomena there is considerable individual variation. There is as yet no practical method for predicting exactly when a particular animal will ovulate. In animals which ordinarily produce only one egg during the heat period, the breeder's problem is to ensure that large numbers of vigorous fresh sperm will be present in the Fallopian tubes at the time of ovulation. In the sow, the theoretically optimum time would be shortly before the majority of the ova are liberated. In the other farm animals fertilization is an all or none phenomenon, since only one ovum is ordinarily involved. In the sow pregnancy may occur even though the percentage of eggs fertilized may be very low. Breeding swine either too early or too late in the heat period may have an effect on litter size.

Cows and ewes should be mated during the latter part of the heat period. The optimum time is shortly after the middle of estrus. However, since heat is relatively short in those species, random breeding at any time during heat will result in fair breeding efficiency. In the sow and mare the longer heat period may influence fertility. At the Purdue Station it is recommended that gilts be bred early during the second day of heat and that sows be mated sometime during the second day. Sows tend to stay in heat longer than gilts and can be mated a little later. These recommendations are made with the assumption that the breeder will try the animals each day to determine the presence of estrus. In swine, if the boar is not being used too heavily, conception rate and litter size can usually be improved by mating the females more than once during heat. Mares have the lowest conception rate of all the farm animals. This is due to the limited survival time of sperm in the female and to the uncertainty of the length of heat and the time of ovulation in any particular mare. Studies by the writer showed that the highest conception rate occurred when the mares were either naturally or artificially inseminated each day beginning on the second day of heat and

continuing until the end of estrus. This system is not practical under farm conditions. Breeding during the third, fourth, and fifth days of heat produced excellent results. Some breeders report equal success by breeding every other day beginning on the third day of heat. If a mare can be bred only once, the fourth day of heat is usually the best.

Vitality of Ova.—The survival of sperm within the female reproductive organs is long by comparison with the viability of ova. The early work of Lewis at the Oklahoma Station in 1911 is classic for its type. Of 13 sows force-bred a total of 34 times following the cessation of estrus, only 1 became pregnant. Lewis correctly concluded that the ovum does not retain its vitality for more than a few hours following ovulation. More recent studies have shown that not only is the life of the ovum short but that developmental abnormalities may be related to the age of the egg at the time of fertilization. In the guinea pig Blandau and Young (1939) found that when fertilization was delayed for 8 hours following ovulation there was an increase in the number of sterile inseminations, a decrease in litter size, and an increase in abnormal pregnancies. No normal development followed insemination more than 20 hours after ovulation, and complete sterility occurred after 32 hours. Similar results were obtained in the rat (Blandau and Jordan, 1941). Records of cattle inseminations have consistently shown that very poor conception occurs when insemination is carried out 12 hours or more following the end of heat (Trimberger and Davis, 1943).

Superovulation.—Following the discovery of the gonadotropic principles, numerous attempts to induce estrus and ovulation have been made. For the most part the studies have been concerned with the induction of normal estrual cycles and ovulation rates typical of the species. However, a number of investigations of superovulation, the production of large numbers of ova, have been carried out.

It was shown that certain gonadotropic materials would produce superovulation in rats and mice, that many of the eggs were fertilized, that there was a relatively high rate of embryonic mortality, but that larger than normal litters could be produced (Engle, 1927; Cole, 1937; Evans and Simpson, 1940).

This problem has been investigated in both cattle and sheep at the University of Wisconsin by Casida *et al.* (1940–1944). Twenty-four ewes treated with follicle-stimulating extracts had a total of 576 corpora lutea, and 357 ova were recovered. All the ewes were artificially inseminated. Seven of the animals had no fertilized ova, and 17 of them yielded from 2 to 19 ova in varying stages of cleavage. The responses obtained varied with the gonadotropins used and the stage of the estrual cycle at the time of treatment (Murphree *et al.*, 1944).

Following the demonstration that superovulation and fertilization could be obtained, a study of the survival of induced multiple pregnancies was made (Casida *et al.*, 1944). Superovulation was induced in 25 ewes. It was found that at 2 to 5 days following insemination there were 9.2 normal embryos per ewe, 3.4 normal embryos at 14 to 27 days and an average of 0.8 normal embryos at 30 to 37 days of gestation. No lambs were produced. Similar results had previously been obtained with cattle (Casida *et al.*, 1943).

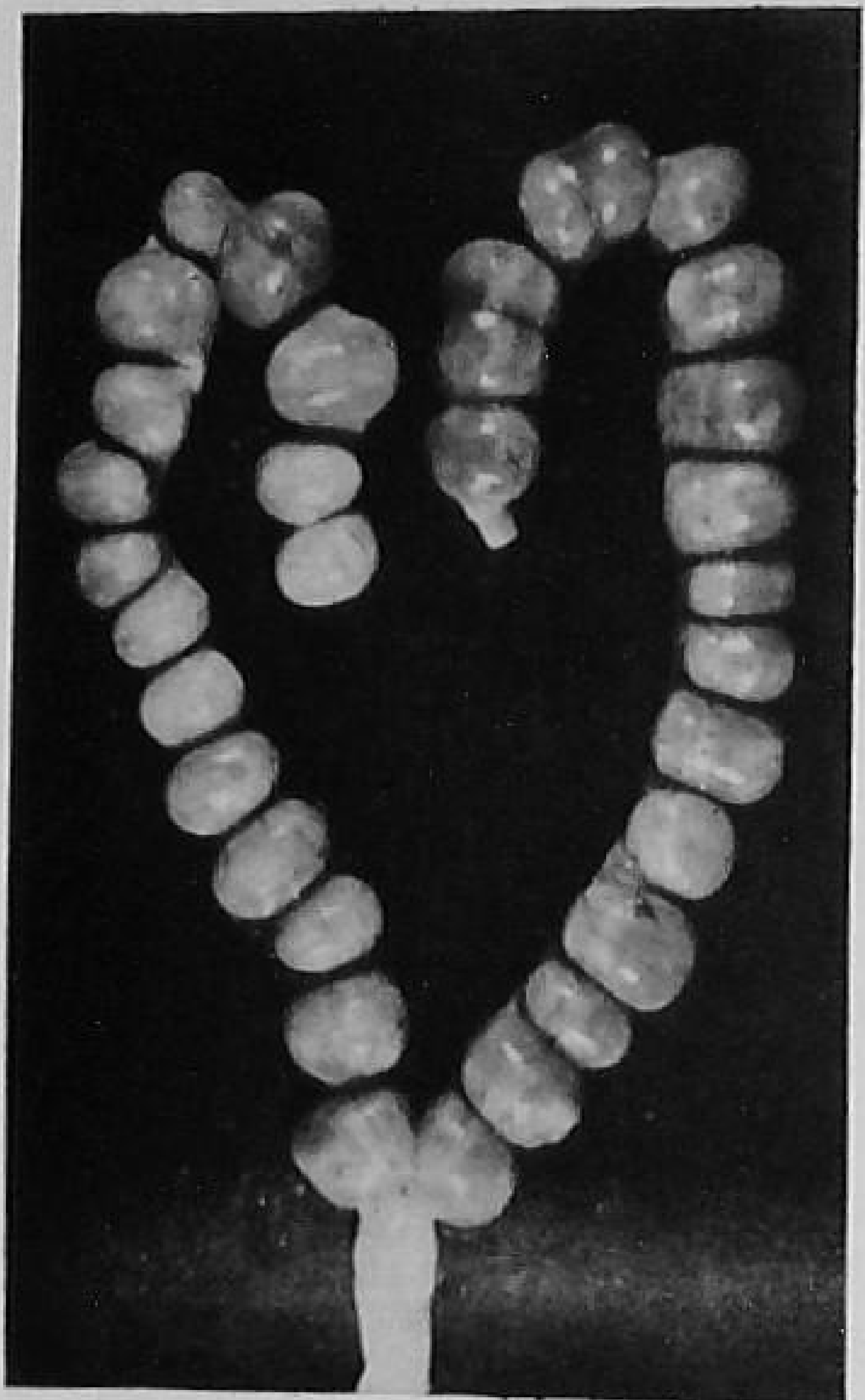

FIG. 51.—Superovulation in the rabbit. Uterus of rabbit 13 days after termination of treatment with gonadotropins there were 33 placental sites of which 18 contained normal embryos, 4 contained degenerate embryos, and the rest were empty. (*Courtesy of Drs. Casida, Warwick, and Murphree, University of Wisconsin.*)

There is considerable doubt as to the desirability of multiple pregnancies in most species of farm animals. In the horse, twins or triplets are very undesirable. Twins are seldom successfully raised and most frequently both die. In cattle twins occur once in every 50 or 60 births. The high incidence of the freemartin condition in twins of opposite sexes, the increased mortality rate of twins, and the fact that there seem to be more difficulties in cows which produce twins, all combine to make multiple births of questionable value in practical cattle production.

Multiple births are considered desirable in both sheep and swine, but even in these species there are problems. Under range conditions single lambs are often preferred because of their greater size and vigor. In some cases, high prolificacy of swine has been associated with reduced birth weight of the pigs and thus a lower rate of survival. This problem is not general in swine, but is mentioned because there are limits to prolificacy.

It is possible that the capacity of the uterus, in regard to size, circulation efficiency, nutritive and excretory capacity, may be limiting factors. As pointed out by the Wisconsin group, superovulation may result in the production of abnormal ova, capable of fertilization but not of normal intrauterine development.

Castration.—This operation in the female is generally called *spaying*. It has not been practiced to as great an extent as in the male and is becoming rare in practical livestock production. One of the reasons is that any operation which involves entering the abdominal cavity necessitates a skilled surgeon and always involves risk. The chief reason for the decline in spayed animals is that the results are not so striking as in castration of the male. Many studies of its value have been made; the results at the Purdue Station are typical, although not original. Spayed beef heifers tend to have better finished carcasses than normal females, but they do not grow so rapidly nor do they utilize feed so efficiently. It is doubtful if the practice is economically sound.

This terminates, temporarily, the discussion of the primary organs of reproduction in the female, the ovaries. We will return to them again when fertilization and implantation are discussed and in the consideration of fertility, sterility, and breeding efficiency in subsequent chapters.

Fallopian Tubes.—The Fallopian tubes, ovarian tubes, or oviducts, act as excretory ducts of the ovaries, conveying ova from the ovaries to the uterus. They are not, however, in direct continuity with the glands but rather partly in continuity with and partly attached to them, both ovaries and oviducts being suspended in a fold of the broad ligament, the mesosalpinx. Their anterior ends open into the peritoneal cavity, and posteriorly they join the horns of the uterus or the uterus proper.

Their analogues in the male are the vasa deferentia. The Fallopian tubes consist of an inner mucosa and outside this a circular and a longitudinal muscularis and an external serous coat. They are firm to the touch and have a diameter of about 0.1 in. in the cow. The fimbriated, or funnel-shaped, end of the oviduct nearest the ovary is called the *infundibulum*. The middle portion consists of the dilated ampulla and the constricted isthmus, whereas the portion entering the horn of the uterus is called the *intramural* portion. The mucosa of the oviduct is thrown up into folds and is richly supplied with lymphatics and thin-walled blood vessels, indicating a secretory activity. The epithelial lining of the oviduct is often ciliated, and the ciliary motion is chiefly toward the uterus. Spermatozoa that are deposited in the vagina or uterus at copulation pass up these tubes to their upper end, where fertilization usually takes place as soon as the ovum is liberated.

Experimental removal of one ovary and tying off of the opposite oviduct has been followed by pregnancy. In some way, in other words, the egg produced by one ovary moved across the peritoneal cavity to the other oviduct and on down to the uterus. Dukes suggests that this may be due to the action of the cilia in the infundibulum setting up a current in the peritoneal fluid, the cilia beating toward the uterus.

The fertilized ovum or zygote passes down one of these tubes in from 3 to 4 days in domestic animals to find lodgment in a horn or in the body of the uterus. For this purpose, aid is perhaps derived in some species from the cilia or microscopic fingerlike projections from each of the cells that line the inside of the oviduct and by a waving motion tending to push the ovum downward. In other species, however, cilia are lacking in the oviducts, so that the downward passage of the zygote is probably here referable to the peristaltic action of the musculature of the tubes, even though this is made up of small waves rather than one continuous wave. Like the rest of the female genital tract, the oviducts and their glands become more active at estrus. Fallopian tubes, the lumina of

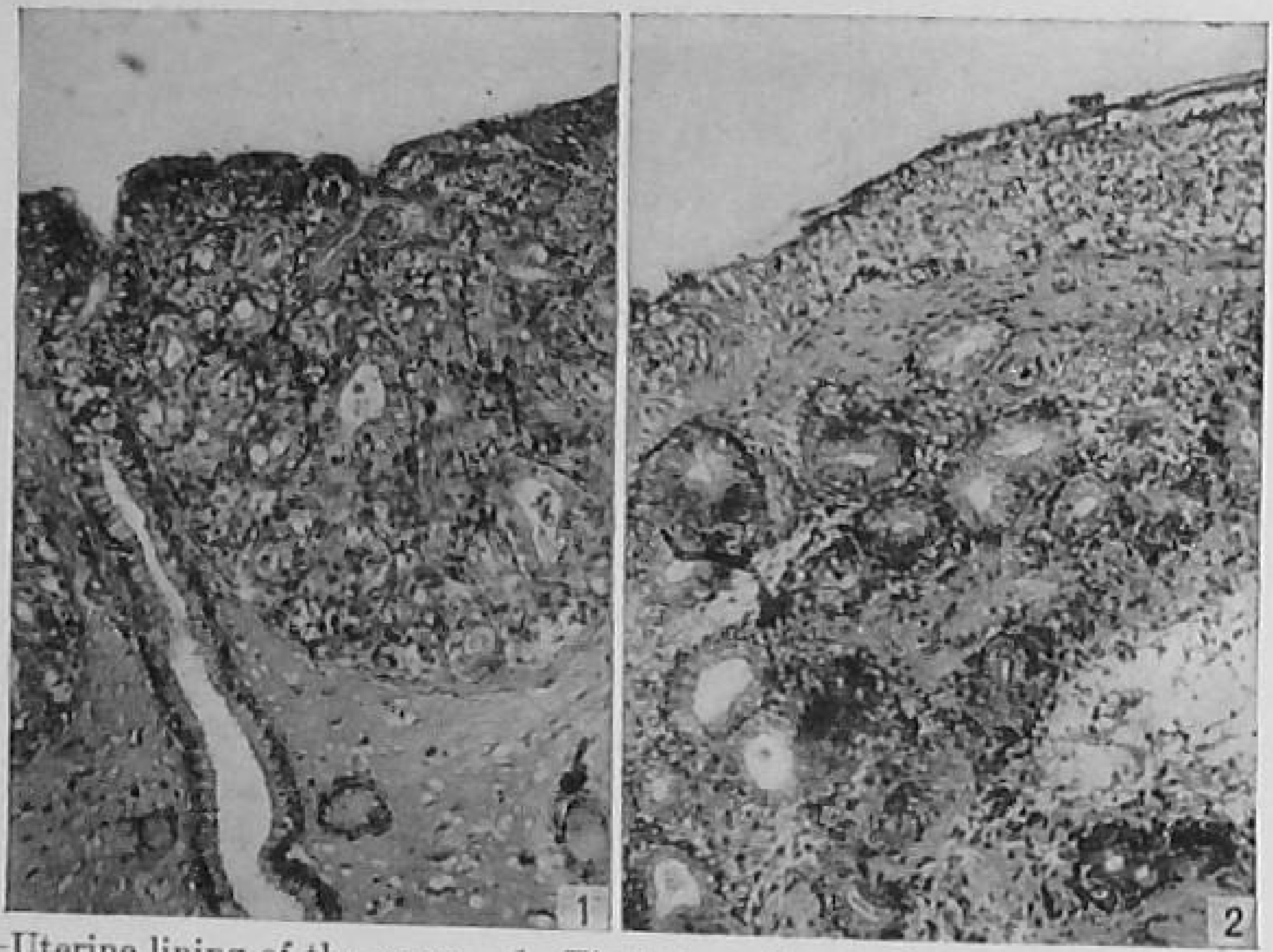

FIG. 52.—Uterine lining of the mare. 1. First day after foaling, endometrium specialized for pregnancy. 2. First day of foal heat, endometrium not yet repaired following foaling.

which are smaller than the lead in a pencil and greatly convoluted, act somewhat in the nature of a seal, thus preventing anything harmful passing down into the pregnant uterus. It can readily be seen, too, that, if infection of any sort once found lodgment here, it would be exceedingly difficult to combat or to eliminate. The most usual type of sterilization operation in woman consists of the severing and tying off of the oviducts so that sperm are not able to come into contact with the egg.

Uterus and Horns.—The oviducts in the higher animals terminate in the horns of the uterus, and the two horns terminate in the body of the uterus. It is here, of course, that the embryo undergoes its prenatal development. In the human, the horns of the uterus are practically lacking. In the mare the body of the uterus is nearly equal in length to that of the horns, whereas in the cow, ewe, and sow the body is short and

the horns long. The horns, or cornua, are long and straight in the dog and cat, long and coiled or folded in the sow, and long and curved, somewhat like a ram's horns, in the cow, ewe, and goat. The horns and uterus proper are lined with a highly vascularized mucosa bounded by two layers of muscle fibers, the inner circular and the outer longitudinal layers. This muscular structure provides the uterus with the degree of elasticity necessary for pregnancy and also provides the means for the final expulsion of the fetus at time of parturition.

The external covering of the horns and uterus is the serosa. The mucosa of the uterus is highly vascularized and contains many glands and lymph spaces. During sexually mature life it is undergoing rhythmic changes due to the heat periods, the inner surface being renewed periodically preparatory to the release of eggs from ovaries. The glands increase in size and activity at this time also. The fertilized egg descends the oviduct and finds lodgment in or on the uterine mucosa. Parts of the inner uterine wall become modified, forming the maternal part of the placenta by means of which the embryo receives its materials for growth. This may be a circular or disklike area, as in woman and the mare, a zone or band, as in the bitch or cat, or rows of cotyledons or caruncles, as in the cow and ewe.

Cervix.—The uterus terminates posteriorly in the cervix, or neck of the womb. This is a very thick-walled portion of the genital tract. It is lined with simple epithelial cells that secrete copious amounts of mucus into the small canal passing through the cervix. The thick muscular walls are thrown into many folds that expand at time of parturition to allow passage of the fetus and then retract in a few days to their contracted state. The cervix forms an effective seal at the posterior end of the uterus.

In the mare, the cervix is 2 to 3 in. long and 1½ in. in diameter. The cervical canal is straight and never fully closed in the nonpregnant state. In the cow it is about 4 in. long with a wall 1 in. or more in thickness and is always tightly contracted except at parturition. The canal through the cow's cervix is spiral, folds of tissue being thrown back on each other making it difficult to dilate or to insert an instrument of any sort. In the ewe, the cervix is about 1½ in. in length, and the lumen is tightly contracted and difficult of entrance as in the cow, whereas in the sow it is about 4 in. long, partly occluded by rounded prominences on its interior and has no intravaginal projection as found in the mare, cow, and ewe.

The character of the mucus secreted by the cervix varies considerably at different times of the reproduction cycle. During estrus, the mucus is thin and watery, the cervix also somewhat relaxed. Both these con-

ditions render passage of the semen into the uterus easier. Following heat, the mucus thickens and remains in this condition until the next heat period. Following the onset of pregnancy, the cervical mucus becomes very thick, forming a more or less solid and permanent plug that seals the cervix and thus protects the developing embryo. Disturbance of this plug is often followed by abortion, but the reaction here is quite variable among both individuals and species. Owing to its structure, especially in the cow, pathological conditions in the cervix are particularly hard to treat.

Vagina.—From the cervix posteriorly to the urogenital sinus or vestibule, the female genital tract is termed the *vagina*. In farm animals it

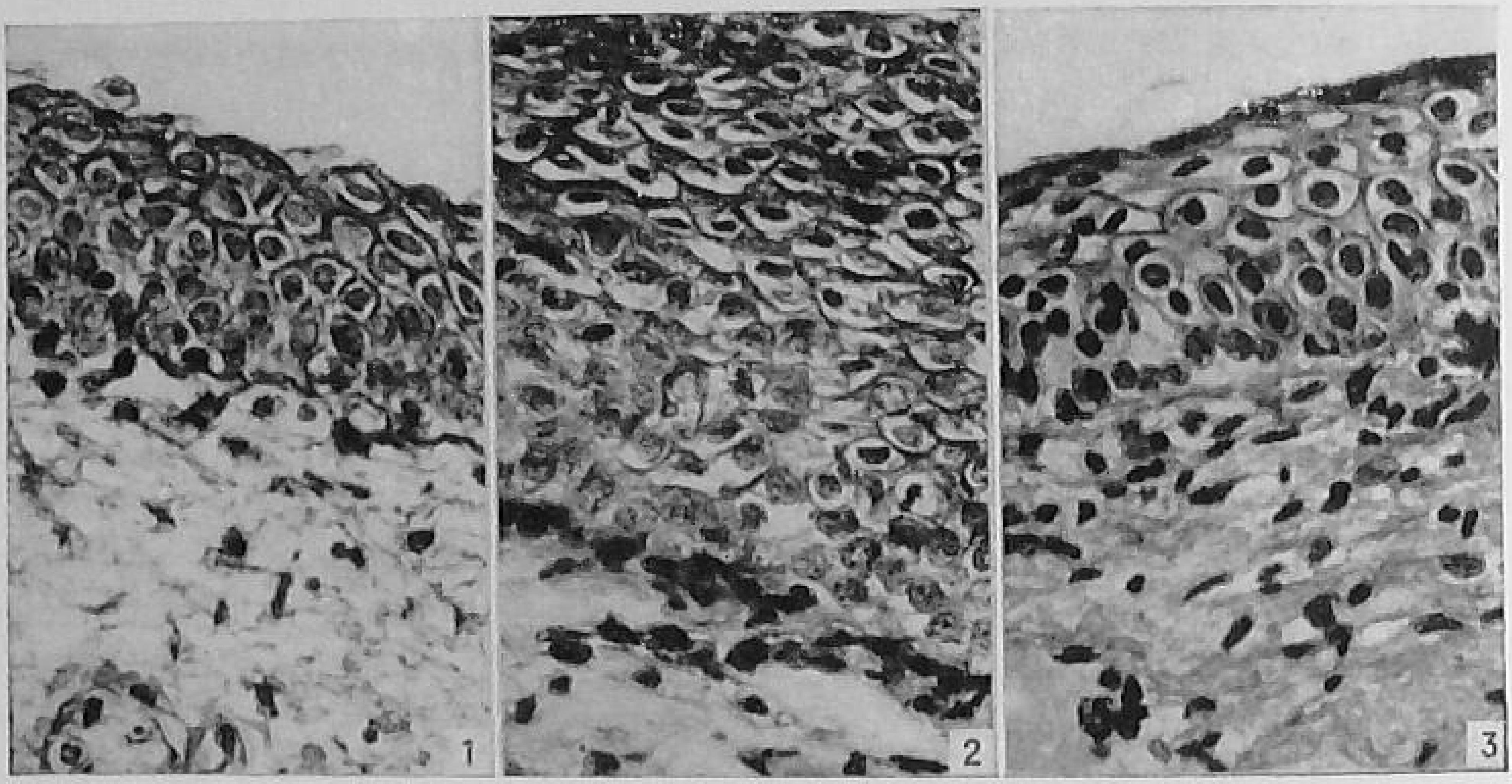

Fig. 53.—Changes in the vaginal epithelium of the mare during the estrual cycle. 1. First day of estrus. 2. Seventh day of estrus, observe increased number of epithelial cells and flattening of surface cells. 3. Five days after estrus.

lies horizontally below the rectum and above the bladder. This portion of the tract is relatively simple both in structure and function. It consists anatomically of the usual three layers of tissue: mucosa, muscularis, and serosa. The epithelial lining of the vagina is very responsive to cyclic sexual changes, and these changes have been intensively studied and correlated with the phenomena of estrus, ovulation, etc., in laboratory animals and in woman. During estrus the cellular epithelial lining of the vagina proliferates, becomes highly stratified. During interestrus it is less active and consists of fewer layers of cells. In the mare the vagina is about 6 to 8 in. long; in the cow, 8 to 10 in.; in the ewe, 3 to 4 in.; in the sow, 4 to 5 in. The vagina generally becomes longer during the pregnant state.

The function of the vagina is twofold: (1) to receive the intromittent

organ of the male in copulation and probably in most cases the ejaculate also, and (2) to provide a passage for the fully developed fetus at term.

Vulva and Clitoris.—The female genital tract terminates posteriorly in the vulva or external orifice. With the onset of heat, or estrus, these structures become congested and enlarged, particularly in the sow, somewhat less so in the cow, the mare, and the ewe. The clitoris, the small erectile organ homologous to the penis in the male, is situated just inside the portion of the vulva farthest removed from the anus. Sufficient stimulation of the clitoris results in a sexual orgasm in the female.

Fertilization.—Hormones from the anterior pituitary cause a number

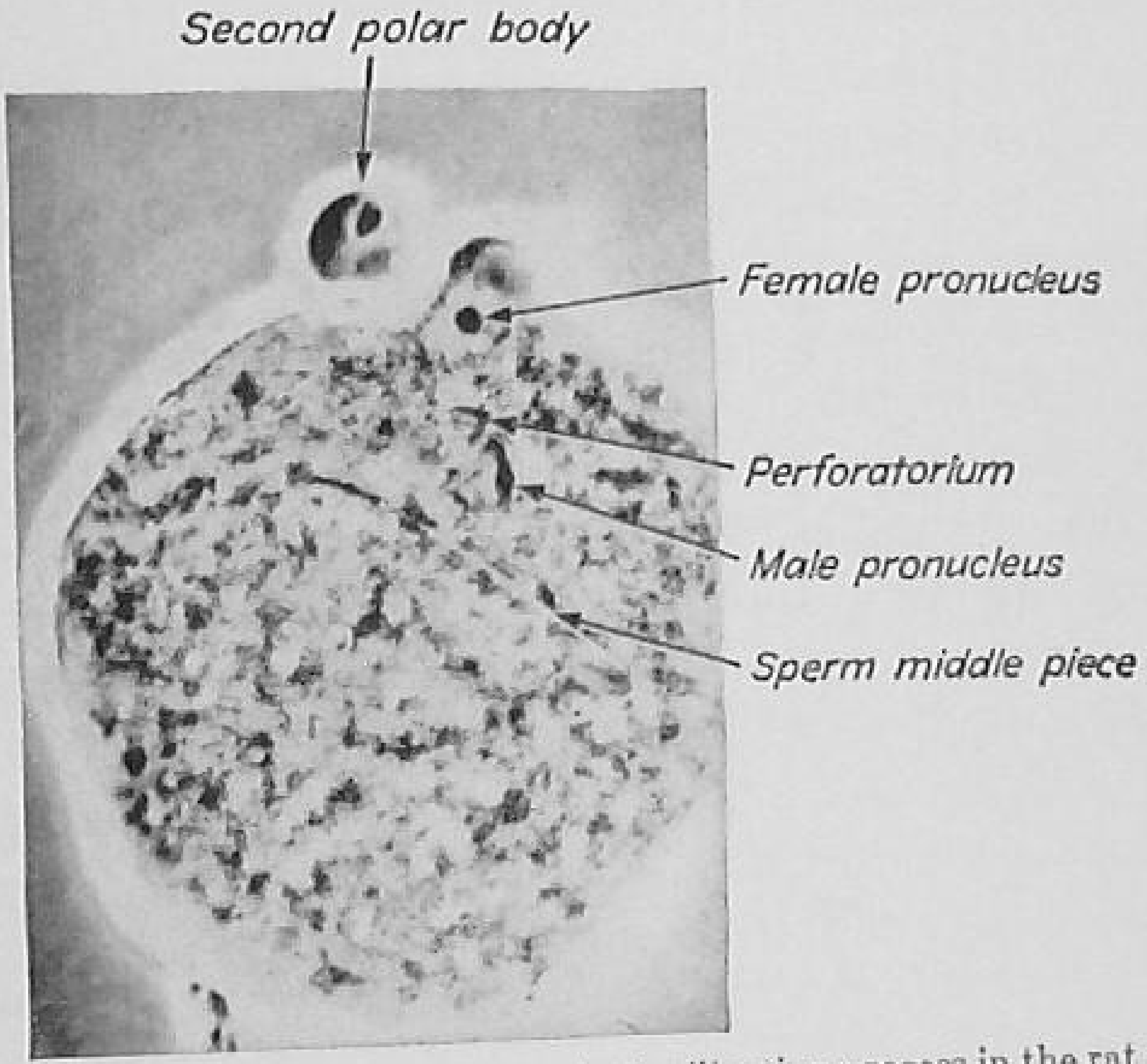

FIG. 54.—A rare photomicrograph of the early fertilization process in the rat taken with the phase microscope. (*Courtesy of Dr. Richard J. Blandau, University of Washington, School of Medicine.*)

of follicles to begin their final rapid growth and maturing processes. Eventually one or several (depending on individuality and species) follicles become fully mature, a process which includes the reduction in the number of chromosomes to the haploid number through the budding off of a polar body containing one member of each pair of chromosomes. The follicle finally ruptures, and the egg is liberated during estrus. At this time the female will accept service by the male, and billions of spermatozoa are introduced into the distal end of the vagina, into the cervix, or possibly in some species directly into the uterus. In the course of a very few hours masses of spermatozoa have been transported through the uterus and tubes to the upper end of the latter.

The ovum drops, or is swept, into the infundibulum, and one spermatozoon immediately pierces it. This stimulates the ovum to throw off the

second polar body. Immediately following, the tail of the sperm is dropped or discarded, the male and the female pronuclei approach each other within the ovum, the centrosome brought in by the middle piece of the sperm divides, a portion moving to each pole of the cell, and the paternal and maternal chromosomes finally become arranged in the equatorial plane. This process is known as *fertilization* and is completed with the fusion of the male and female pronuclei and the arrangement of the chromosomes in the equatorial plane. It is probable that fertilization is completed within a few hours after service by a normal male on a female in estrus; other sperm may penetrate the zona pellucida but only one enters the oöplasm to effect fertilization.

In recent years mammalian ova, especially from the rabbit, have been secured and have been fertilized in test tubes, the process having been observed. They can then be inserted into the uterus of a properly stimulated female, and embryonic development will proceed normally to term in the foster mother. Pincus (1939) has recently caused development of the rabbit ovum without stimulation of the sperm. This is the long-sought mammalian parthenogenesis and occurred, according to Pincus, because of an early restoration of the diploid number of chromosomes through nuclear division without cell division.

In the multiparous animals it is seldom that all the eggs liberated are fertilized and implanted, the loss in the sow having been determined to average 20 to 30 per cent and to run as high as 50 per cent. Multiple ovulations in the cow and mare are also known to be more numerous than multiple births, which in these species is a good thing. It is better, too, from a practical standpoint, for a sow to have 10 or 12 good-sized vigorous pigs than 20 or 25 small, weak ones, the large majority of which generally die very early.

The fertilized egg, or zygote, immediately begins (1) to grow by cell division and (2) to descend the Fallopian tube into a horn or the uterus proper. The egg is huge compared with other body cells because of its stored yolk. Its early segmentation does not involve an increase in size but rather an increase in cell numbers and a consequent reduction in the size of the cells to that characteristic of other body cells of the species. Cell divisions proceed at first at the rate of one or two a day. The passage down the tube is probably effected by both ciliary and muscular activities of the oviduct and takes from 3 to 4 days. The oviduct also produces a secretion that may help to nourish the egg in its passage downward. Normally the mass of cells reaches a horn or the uterus proper (though ovarian, abdominal, and tubal pregnancies occur now and then) and becomes attached to the uterine mucosa where embryonic development proceeds.

Attachment generally occurs in the larger farm animals in the horn of the uterus corresponding to the ovary that contains the corpus luteum, but many cases of migration and implantation in the opposite horn have been recorded. In multiparous animals like the sow, implantations occur at more or less regular intervals throughout the two horns, regardless of the fact that most of the eggs may have been produced by one ovary or, as demonstrated by Warwick, after removal of one ovary. The exact mechanism regulating the site of implantation is at present unknown.

Corpus Luteum.—The corpus luteum (yellow body) is an intermittent or periodic gland of internal secretion that is formed within the follicle after ovulation. Upon rupture of the follicle and liberation of the ovum, there ensues a rapid vascularization of the granulosa and theca cells that surrounded the follicle and sometimes an escape of blood from the theca into the follicular cavity. The cavity closes over and with the retained blood clot is known as the *corpus hemorrhagicum*, which is the earliest stage in the development of the corpus luteum. The connective-tissue cells of the theca folliculi, which have arisen from the ovarian stroma surrounding the follicles, gradually grow in and partially fill the follicular cavity, the blood clot gradually undergoing absorption. The granulosa cells of the undischarged follicle hypertrophy. The rapidly multiplying cells of the theca, under stimulation of LH from the anterior pituitary, absorb yellow lipoid pigment and fat droplets, which give to the corpus luteum its characteristic yellow color, which varies, however, in different species. Blood vessels are carried in with the ingrowing tissue from the theca, making the corpus luteum a highly vascularized gland. The corpus luteum grows quickly, soon filling the follicular space and usually protruding from the ovary, its later growth being due to enlargement of the cells rather than to cell multiplication.

If the animal conceives, the corpus luteum continues to enlarge until about the middle of the gestation period. It then often begins to shrink in size and to decrease in secretory activity until it finally degenerates and becomes the corpus albicans. In some species it is not wholly absorbed until a considerable time after parturition. If conception does not occur, the corpus luteum does not grow so large, and progesterone secretion declines before the onset of the next estrual period.

The functions of the corpus luteum hormone, progesterone, are as follows: (1) progestational changes in the endometrium of the uterus that are necessary to sensitize the uterine wall before implantation of the morula can take place as well as the early development of the placenta, (2) the regulation of the estrous cycle by preventing estrus and ovulation until the corpus luteum reaches a certain stage of atrophy, (3) the maintenance of pregnancy, (4) to assist in the relaxation of the pelvis at

parturition, and (5) some participation, it seems, in the development of the mammary gland.

The amount of luteal tissue necessary to lead to successful implantation has been determined for some species. It has been shown in many species that removal of the corpus luteum shortens the sexual cycle by quickly inducing the next heat period, which in the cow generally follows within 48 hours.

In many species removal of the corpus luteum during pregnancy results in the absorption of the fetus or an abortion within 1 to 10 or 12 days. If performed very soon after fertilization, abortion or absorption is practically certain to follow. Some species can evidently safely dispense with the corpus luteum much earlier than others, and in those cases it is thought that the placenta may then take over some of the functions of the missing corpus luteum, for the relaxation of the pelvic muscles occurs normally as does the development of the mammary glands.

Placenta.—The placenta consists of two parts: (1) the maternal placenta, which is of maternal origin, and (2) the fetal placenta, which is of fetal origin. The fertilized egg, or zygote, obtains its nourishment at first from its own stored yolk and perhaps also from its investing envelopes, the zona pellucida and the corona radiata. Next it subsists on materials secreted by the uterine glands, absorbed directly at first and obtained later by means of the yolk sac. Finally, it becomes embedded in or attached to the uterine wall. The placenta is developed through which food materials pass inward to the embryo, and waste materials pass outward from it by means of the placental blood vessels.

Following segmentation, which produces a solid mass of cells (morula stage), a central cavity is formed within the mass of cells (blastula stage.) Then there ensues an invagination (gastrula stage), and the embryo proper develops from the invaginated cells. The portion remaining outside is called the *trophoblast.* At first each blastomere is nourished independently, but, following invagination, the trophoblast is concerned wholly with the nourishment of the embryo that is to be elaborated. The fusing of the external wall of the allantois, an outpouching from the hindgut region, with the trophoblast produces the chorion, or afterbirth. The trophoblast is highly vascularized by outgrowths from the blood vessels of the allantois.

In the pig, the blastocysts are spherical for 10 days, but then they rapidly elongate, and by the fourteenth day they together fill the whole length of the uterus. Foldings appear in the trophoblast that fit into folds of the uterus, which increase the area of contact. The trophoblast fits closely to the surface epithelium of the uterus and sends protoplasmic processes between the cells and perhaps down to the underlying layer of

dilated capillaries. Villi do not form in the pig, and the uterine mucosa has no special cotyledonary areas. The placenta of the pig is, therefore, of the contact type (semiplacenta) in contrast to the burrowing type (true placenta), *e.g.*, human. Materials secreted by the uterine glands are absorbed by the trophoblast and transported to the embryo by means of the allantoic blood vessels.

In the mare the lymphatic system of the uterine mucosa is greatly developed, and villi are found in the allantois that fit into tiny crypts of the uterine wall.

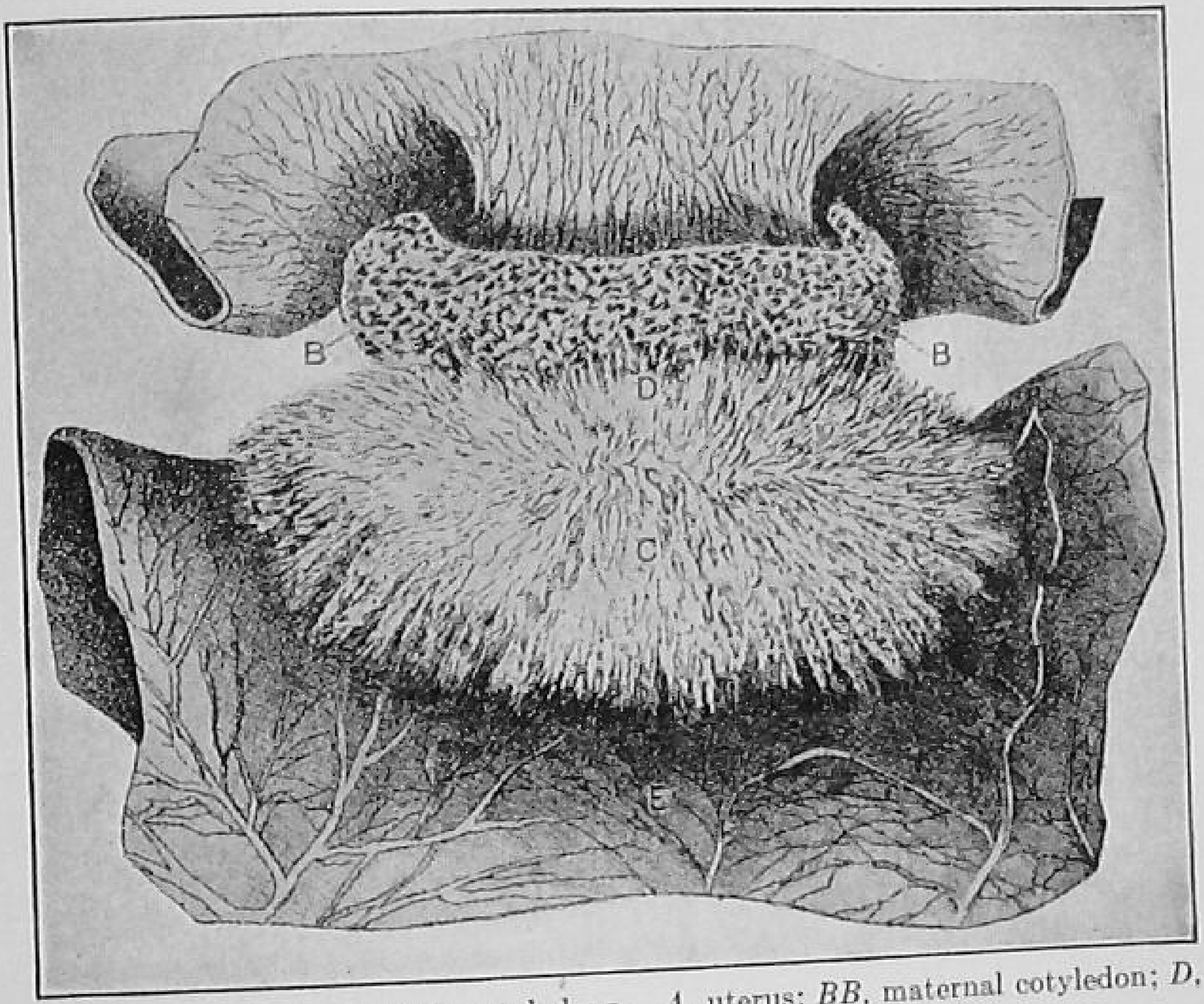

Fig. 55.—Pregnant uterus with cotyledons. *A*, uterus; *BB*, maternal cotyledon; *D*, fetal cotyledon. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

In the cow and the ewe there are many special points of attachment between the chorion and the uterine wall. These are called cotyledons (buttons), and these species are, therefore, of the polycotyledonary type. There are 70 to 130 cotyledons in the ewe and cow. During pregnancy the cotyledons become spongy, owing to increased vascularization and the enlargement of the lymphatics. Villi containing blood vessels from the allantois grow out from the cotyledonary areas of the trophoblast and become embedded in the tissues of the cotyledons of the uterus. The uterine glands in the intercotyledonary areas as well as the surface epithelium also secrete copiously during pregnancy. This secretion, together with its contained formed constituents (red-blood corpuscles,

leucocytes, fat globules, salts, glycogen, etc.) from the blood and lymph systems, is known as uterine milk. It seems probable that the exchange of oxygen and carbon dioxide is effected in the cotyledons, where glands are absent and where the maternal and fetal blood systems come into close contact.

The function of the placenta is, of course, the elaboration of the materials necessary for fetal development and the development of a transporting system for conveying food materials to the embryo or fetus as well as waste products away from it. It should be remembered that

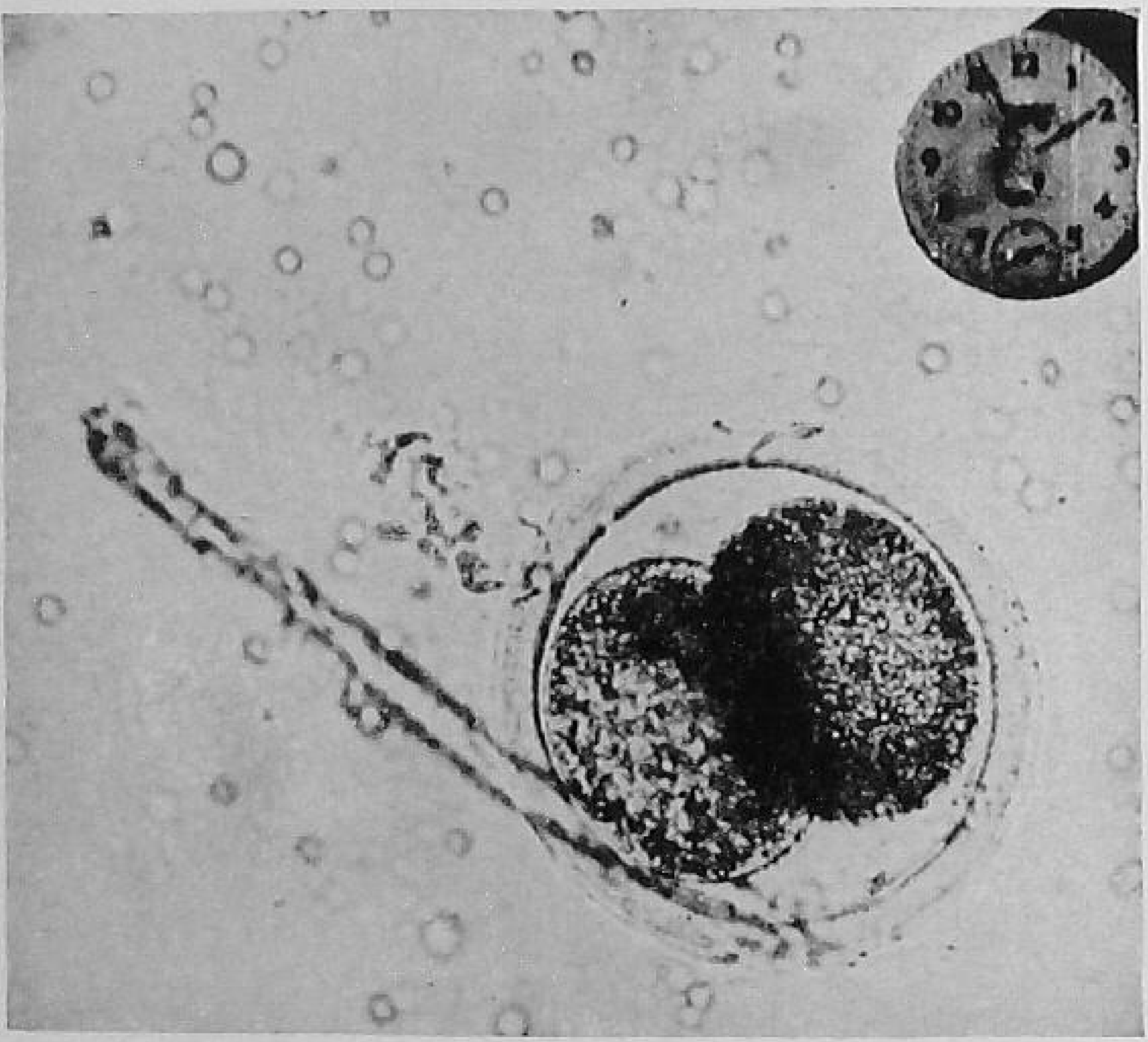

FIG. 56.—Embryonic calf at the two-cell stage. (*Courtesy Bureau of Dairy Industry, U.S. Department of Agriculture, and Carnegie Institution of Washington.*)

the mother contributes no blood as such to the embryo. If we think of an island out in midstream as the embryo, then the intervening river and boats plying back and forth might be thought of as the placenta foetalis and the sandy beach of the mainland as the placenta uterina.

The placenta performs an endocrine function as well, and in some species secretes estrogens, progesterone, and gonadotropic hormones.

Embryological Development.—As noted previously, fertilization, or the union of the male and female pronuclei, each with its haploid number of chromosomes, generally occurs in the Fallopian tube following ovulation. The zygote within the surrounding capsule, or zona pellucida, immediately starts its descent to the uterus. Cell division is inaugurated by the entrance of the sperm and continues during the descent. The time

required for the developing zygote to traverse the oviduct probably varies somewhat in different species but consumes a period ranging from 1 or 2 up to several days. During this time the egg lives and grows upon its own stored nourishment found in the yolk.

Upon entrance into the uterus, the group of cells, probably in the morula stage, takes lodgment upon or in the uterine wall, absorbing nourishment for growth from the uterine secretions until its own developing extraembryonic membranes can set up a connection with the blood

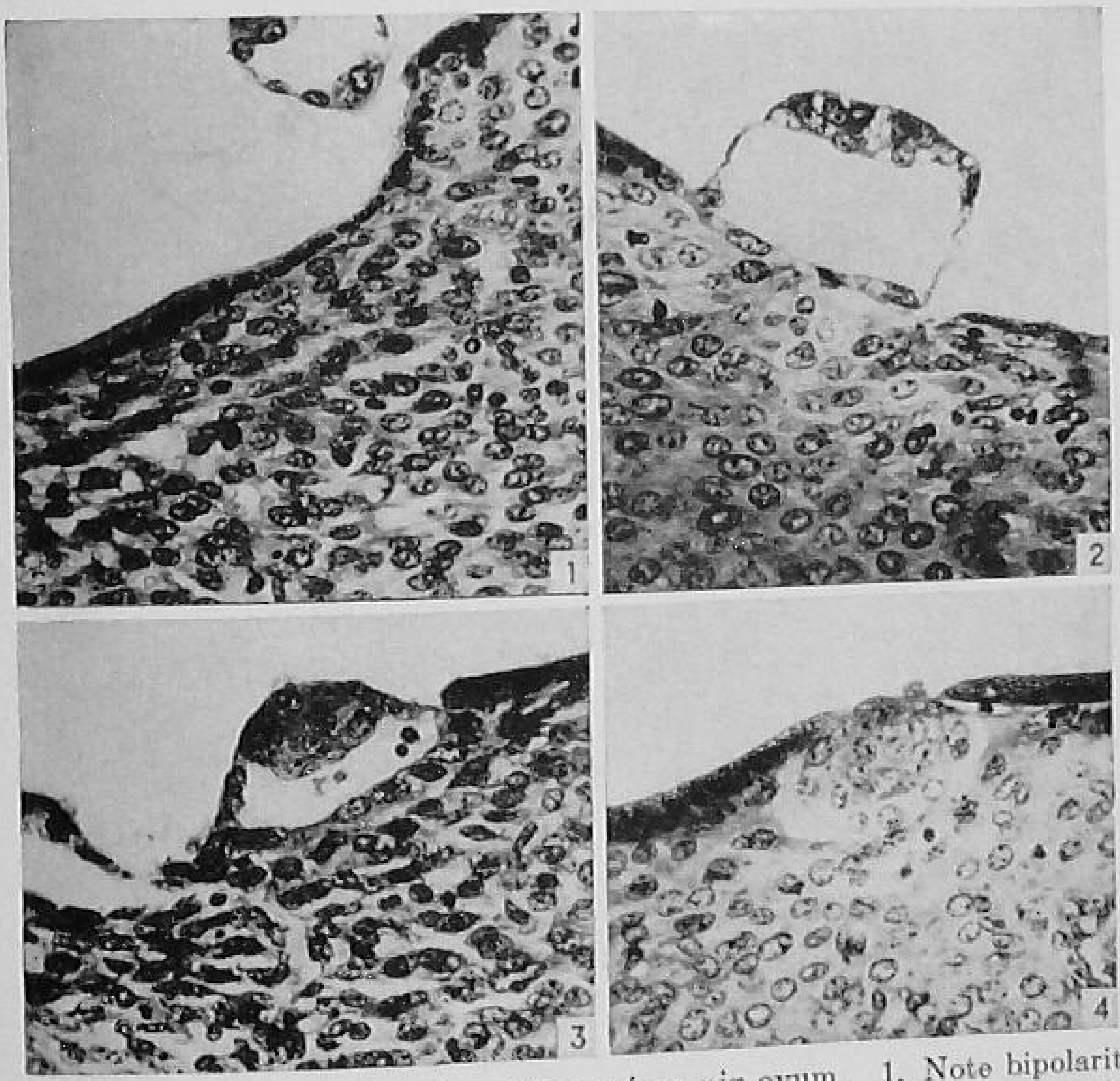

Fig. 57.—Stages in the implantation of the guinea pig ovum. 1. Note bipolarity of the ovum and beginning of attachment to the uterine epithelium. 2. Observe loss of nuclei in the uterine epithelium. 3. Implantation approximately one-half completed. 4. Implantation almost completed. (*Courtesy of Dr. Richard J. Blandau, University of Washington, School of Medicine.*)

vessels of the mother's uterus. It should be understood that the nutrition of the embryo is indirect after the initial stages. The embryo lives first upon the stored nutrients in the yolk of the egg, next upon the uterine secretions, then upon materials carried to the placenta in the mother's blood stream, then, in mammals following parturition, upon milk secreted also from the mother's blood, and, finally upon food that the young has learned how to secure for itself. The embryo never gets any blood as such from its mother. It builds up its own blood, a liquid tissue, in the same manner that it builds up all the other tissues of its body, bone,

muscle, nerve, etc., from materials supplied from the mother's blood stream.

The morula, or mulberrylike, stage is succeeded by the blastula, or hollow-sphere, stage, then through an infolding of a portion of the cells the gastrula stage is formed. The outer portion is called the *trophoblast*,

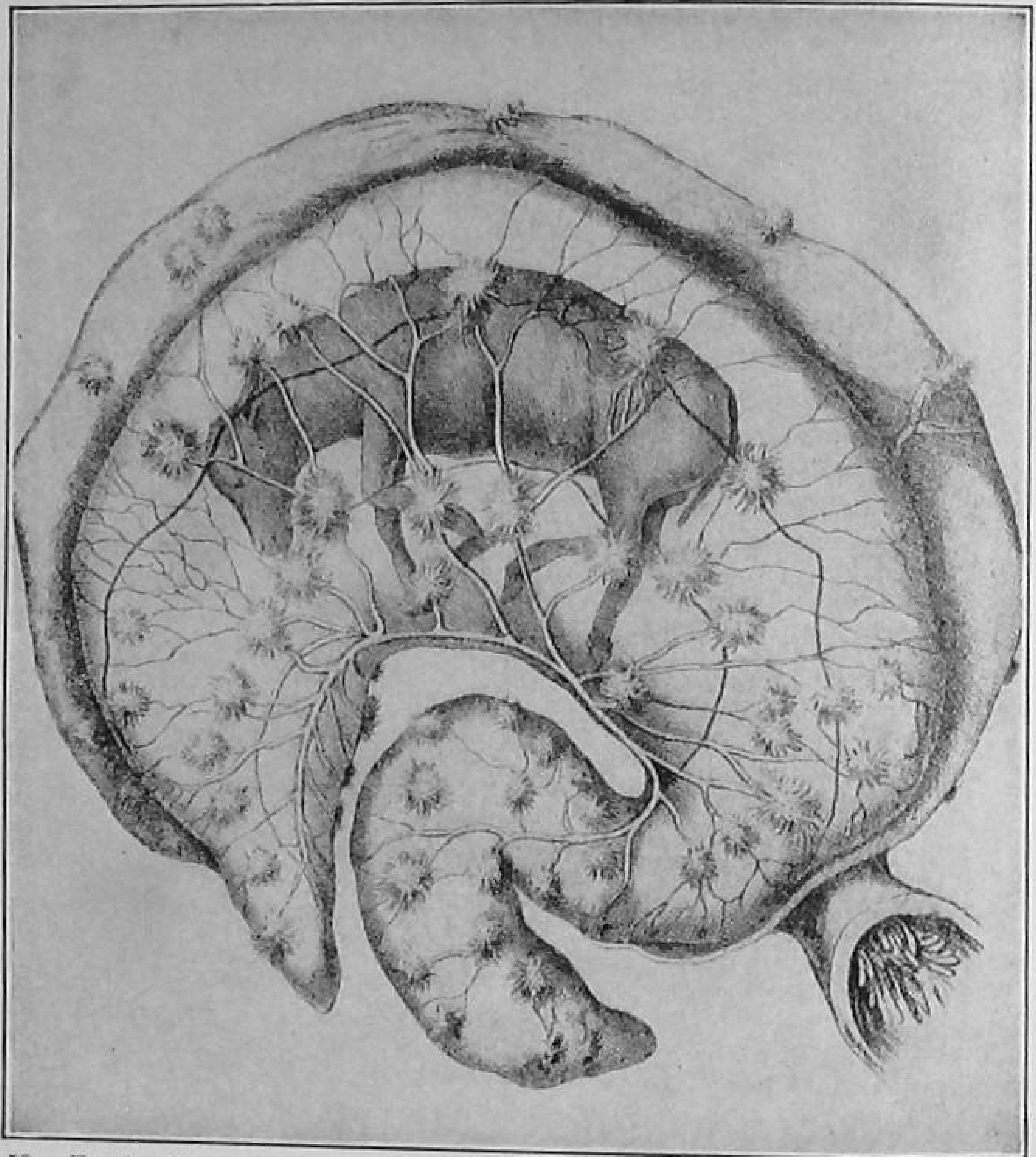

FIG. 58.—Fetal calf within its membranes. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

the embryo proper being retained outside the blastocoele. A yolk sac is developed dorsally, and, although little yolk is present in the egg of mammals, the yolk sac functions for about 3 weeks in the cow, sheep, and pig, and about 6 weeks in the mare, as the medium for supplying nourishment to the embryo. Folds grow out from all sides of the embryo and grow up over it, fusing and enfolding it. This is the amnion, which becomes filled with a watery fluid in which the embryo floats, thus being

protected from concussion. From the hind gut there forms an outpouching that grows out and enfolds the amnion and its contained embryo. This is the allantois, which is also filled with a watery fluid. Its outer wall fuses with the outer wall of the blastocoele, forming the placenta. Food materials are carried down into the maternal placenta, there transfuse into the capillaries of the allantoic circulation, and are carried to the embryo by means of the blood vessels through the umbilical or navel cord. Waste products of the embryo are eliminated by the reverse process. In ruminants, the connection between chorion and uterine mucosa occurs at the cotyledons, or buttons.

Fig. 59.—Bovine monster. Embryonic abnormalities of this type are the exception rather than the rule.

Embryonic development is a complicated and marvelous process. The zygote consists of one minute undifferentiated cell. The baby or calf or pig consists literally of billions of cells that have all come from the original zygote. Some have been differentiated into long-muscle cells, others into secreting cells (liver, pituitary, etc.), others into bone cells, still others into brain cells. We know little at present concerning the cause of this specialization and of the directing forces involved. It seems peculiar from a genetic standpoint, for all the cells of the body have similar chromosomes. Internal stimuli within the cytoplasm of the cells as well as external stimuli in the different regions (organization centers) of the embryo are no doubt operative in bringing about the transformation from the one undifferentiated cell to its billions of differentiated descendants.

Recapitulation.—The ovary, under the influence of the anterior pituitary gonadotropins, produces mature Graafian follicles and ova. The ovary also secretes the female sex hormone, estrogen, in sufficient quantity to cause estrus. Mating ordinarily occurs during heat, and toward the latter part of heat the ovum is liberated from the Graafian follicle as the result of the ovulatory process. Immediately following ovulation a corpus luteum is formed in each ruptured follicle and the hormone progesterone is produced. This is essential if the uterus is to be properly prepared for the establishment and maintenance of pregnancy. If the animal has been mated, the spermatozoa immediately start their journey toward the ovary. They pass through the cervix, body, and horns of the uterus and into the distal ends of the Fallopian tubes where they await and fertilize the ovum or ova. The ovum is transported by the follicular fluid as it oozes from the ruptured follicle into the infundibulum and thence into the Fallopian tube where it must be fertilized by a sperm within a few hours if fertilization is to occur. Ordinarily only one spermatozoon pierces the wall of the ovum and *only* one male pronucleus can unite with the female pronucleus if normal development is to follow. The fertilized ovum now starts its journey down the Fallopian tube and becomes attached to a suitable area of the uterine horn or body for its prenatal development. All these events are under endocrine control and require the most exact morphological and physiological changes and coordination if fertilization and normal intrauterine development are to take place. Embryonic differentiation and fetal development proceed in accordance with the species pattern and end, in mammals, with parturition and lactation.

Chronological Order of Reproductive Physiological Processes.—It is essential for the student and breeder to keep in mind the various physiological processes in the female that are concerned in reproduction. In order of their appearance they are: (1) maturation of the follicle, (2) estrus, (3) copulation, (4) rupture of the follicle, (5) fertilization, (6) formation of corpus luteum, (7) implantation, (8) gestation, (9) parturition, (10) lactation, (11) absorption of the corpus luteum.

Summary.—The female's part in reproduction consists of the secretion of viable ova or eggs in the ovary, their rupture into the infundibulum of the uterine tubes or oviducts, where each is joined by a sperm that contributes paternal determiners of potentialities and incites the marvelous process of embryonic development which will eventuate in a few weeks or months in a new and unique individual. To use again our analogy of an assembly line, the ova originate at the far end of a big tube; they very quickly (if at all) pick up a sperm and then pass into a roomy cavity where all the marvelous parts are slowly fashioned and fitted together

into a completely new individual. As soon as the job is completed, the front door of the uterus, the cervix, which after admitting the sperm was tightly locked to prevent any harmful intrusions, is thrown open and the new individual emerges into a new and strange world. To be successful the breeder must thoroughly understand these processes and the factors affecting any of them for good or ill, in order that breeding operations may be properly timed and conditions made optimum for the eventual bringing into being of superior animals.

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CHAPTER VI

REPRODUCTIVE EFFICIENCY

Reproductive efficiency connotes the optimum effective use of the reproductive powers of *all the animals* in a herd or flock. In the female it is the regular production of offspring over a period of years; in the male, the successful fertilization of the largest number of ova with the fewest possible services. In the following chapter we will describe some of the more common types and causes of sterility and lowered fertility. Unfortunately, reproductive efficiency is not limited only by the conditions which we will discuss. All herds and flocks have some abnormal individuals in which the failure of reproduction can be accounted for. Likewise, in all herds and flocks, all of the apparently normal healthy females do not become pregnant following a single service by a normal healthy male. There is good evidence that these differences in reproductive efficiency are often traceable to differences in breeding management and general care. We should never overlook the fact that our animals are individuals and that the best management of one may not necessarily be the best for another. For the most part livestock management entails the application of common sense directed both by previous experience and by a knowledge of scientific principles. The more thoroughly the principles are understood and the greater the accumulation of experience, the more efficient should be the management. Without good judgment or common sense, neither knowledge nor experience, nor both, will avail to render a livestock-breeding enterprise profitable.

Standards of Reproductive Efficiency.—One of the objectives of every livestock breeder is to produce a pregnancy as the result of each service. In species characterized by single births, as in cattle, this would mean one offspring per service if the process were 100 per cent efficient. In swine, the standard is higher, and we might arbitrarily designate the production of 10 pigs per service as 100 per cent efficiency. This degree of efficiency is occasionally attained, but for the livestock population as a whole the process is far less efficient. It is the authors' opinion that nearly any livestock breeder can increase reproductive efficiency at least 10 per cent by the adoption of currently accepted breeding practices. This increase can be expected in normal animals without the use of any special drugs or therapeutic regimes and involves chiefly the judicious

use and care of sires and the mating of females at the optimum time in respect to ovulation.

The incidence of absolute sterility in cattle has been reported to range from 5 to 7.2 per cent. When those animals with complete reproductive failure are considered separately from those which eventually conceive, the breeding efficiency of the "fertile" animals can be determined. Trimberger and Davis (1943) have summarized the data of 16 different investigations of the breeding efficiency at natural service of nearly 23,000 cattle. In one study of 1,801 cows only 1.32 services per conception were required. Approximately 78 per cent of the cows conceived on the first service, 15 per cent on the second, 4.5 per cent on the third, and 1.7 per cent on the fourth or more services. These data were reported in 1918 and to the authors' knowledge, have not since been equaled in a large group of cattle. At the other extreme are the results of a study of 1,151 cows in which the average services per conception was 2.52. This difference of only one more service per pregnancy may not seem great. When the data are examined, it is seen that only 47.4 of the cows conceived on the first service, 22.4 per cent on the second, 12.7 per cent on the third, and 17.5 per cent required 4 or more services. Delay in the establishment of pregnancy increases the time interval between calvings, decreases the number of offspring per animal, and is accompanied by decreased milk production. When the data from all sources were summarized, it was found that 1.79 services per conception were required. This figure is fairly typical of the average cattle herd in the United States. In occasional well-managed, disease-free herds 70 to 80 per cent of the cows may conceive on the first service. We believe that this degree of efficiency can be attained if the best practices are used. In poorly managed herds, or in animals in which there is a high incidence of genital diseases, breeding efficiency may be less than 40 to 50 per cent. Data on 16,555 cows showed that 64.3 per cent conceived on the first service, 19.9 and 8.5 per cent conceived on the second or third services. Approximately 7 per cent required four or more services. These animals were all naturally mated. The breeding results which are being obtained in artificial insemination associations throughout the United States are very similar to natural service. As a general rule animals which fail to conceive following repeated natural service to a fertile sire cannot be expected to become pregnant when artificial insemination is used.

The breeding efficiency of beef cattle under range conditions is usually expressed in terms of the annual calf crop, since the bulls are allowed to run with the cows during the breeding season. The calf crop on the range may be as low as 40 per cent and occasionally as high as 90 per cent. Baker and Quesenberry (1944) studied the breeding and calving records

at the U.S. Range Livestock Experiment Station, Miles City, Mont., for an 18-year period. The average calf crop during 4,753 cow years was 83.1 per cent. The calf crop varied from 66.1 per cent following the severe drought of 1936 to 92.5 per cent in 1939. An analysis of the data did not show age to be significantly correlated with fertility, but it was revealed that over 50 per cent of the shy breeding cows could be identified by four years of age.

Swine have generally been considered to be the most fertile of all the farm animals. In fact, during the 1930's the prolificacy of swine was considered as one of the leading economic problems of the livestock industry. The data which are available on the breeding efficiency of swine do not tend to support the first statement. Phillips (1939) reported that of 250 sows selected at random from a Bureau of Animal Industry swine herd 16.8 per cent failed to produce litters. Of those which farrowed, 84 per cent conceived on the first service, 12 required two services, 2.5 required three, and 1.5 per cent required four services. In a subsequent report, Phillips and Zeller (1941) presented data on conception failures in 1,354 breeding seasons in six breeds. They found that conception failurés ranged from 13.9 to 36.9 per cent. By estimating the number of ova produced by the different breeds at the time of ovulation and comparing with actual breeding and farrowing data, these workers have attempted to account for the losses of ova which occur. Their estimates of the per cent of ova lost are as follows: "(*a*) failure of conception, 36.4 per cent, (*b*) loss from conception to parturition, 19.9 per cent, (*c*) loss from parturition to weaning, 14.6 per cent, and (*d*) loss at parturition, 2 per cent. This leaves 27.1 per cent of the ova which have the chance to be fertilized represented by live pigs at weaning." When the fertility of swine is considered from this standpoint, reproductive efficiency seems very low. It has been known for many years that in pregnant sows examined in the slaughterhouse only about 70 per cent of the ova which have been produced are represented by normally developing fetuses (Hammond, 1921). Thus, when the fertility of swine is considered in terms of females which do not conceive, those in which few ova are fertilized, the high mortality of fertilized ova, and losses at parturition and prior to weaning, it is evident that a serious and challenging problem exists.

Sheep are commonly flock mated, and the number of services per pregnancy is therefore difficult to ascertain. Fertility is usually expressed in terms of the number or percentage of lambs born to each 100 ewes in one breeding season. Breed differences, plane of nutrition, and general management practices undoubtedly have a great influence on the lamb crop. Under farm-flock conditions in Great Britain, lamb crops of 154

per cent in flushed ewes and 140 per cent in nonflushed ewes have been reported (Nichols, 1926). As reported by Phillips (1939) in the United States the lamb crop of flushed ewes kept under farm conditions was reported as 164 per cent and nonflushed 143 per cent. In range flocks it has been estimated that the average lamb crop is 70 to 80 per cent. During a 10-year period the average services per pregnancy were 2.9 (Shropshire), 2.9 (Southdown), 2.5 (Hampshire), and 1.4 (Karakul) in the U.S. Department of Agriculture flock at Beltsville.

Reproductive failure is more common in the horse than in any other farm animal. Most of the data which are available express fertility in terms of the per cent of mares which foaled during a particular period. Mares are frequently mated more than once during a single heat period, and a large per cent are bred during two or three successive heat periods before they conceive. If the per cent of services which resulted in the birth of living foals was determined, the efficiency would be extremely low.

Data gathered during a 6-year period on the breeding performance of 390 stallions and 28,241 Clydesdale mares showed that 52 per cent of the mares foaled. During a 5-year period 42.3 per cent of 3,640 Thoroughbred mares bred to 43 stallions foaled (Robinson, 1921). In no class of animal is knowledge and skill of more importance than in the horse. In the authors' experience the foal crop can usually be increased from the 50 per cent level to 70 to 75 per cent by proper breeding management (Andrews and McKenzie, 1941). In areas where horse breeding is of importance, as in the Thoroughbred-producing regions, it has been possible to produce living foals from as many as 80 per cent of the mares bred each year.

The Influence of Age on Reproductive Efficiency.—Since age can be accurately measured and is usually closely correlated with growth rate and sexual development, it is not surprising that many practical rule-of-thumb recommendations in regard to age and time of breeding have been developed. At least two important points should be considered by the livestock breeder in the application of such recommendations. All animals must be regarded as individuals. Animals of the same age may differ widely in weight and degree of development and thus differ in readiness for conception. A second problem for consideration is that sexual maturity, or puberty, is not a single point but extends over a considerable period of time, depending on the species concerned and other factors. In the human, for example, Mills (1939) estimated that there is a lag of about 6.5 years between the onset of the menses and the establishment of pregnancy in married Filipino girls. In rats Babcock

et al., (1940) reported that the age at puberty in the female is about 65 days but the normal age for breeding is about 100 days. Even when breeding in rats is delayed until 100 days, however, there is a time lapse of 11.7 days between opportunity of mating and the establishment of pregnancy (Asdell *et al.*, 1941).

The problem of age and breeding efficiency has been widely investigated in cattle and to a lesser extent in swine and sheep. One of the earliest investigations of this problem was begun by Mumford at the Missouri Experiment Station with swine in 1909. Sows bred at 218 days of age farrowed 8.68 pigs per litter, and reached a mature weight of 415 lb. Females bred at 479 days farrowed 8.36 pigs per litter and reached a mature weight of 401 lb., whereas those not mated until 838 days farrowed only 5.62 pigs per litter and reached a mature weight of 384 lb. The *rate* of growth of the early-bred gilts was lowered, presumably because of the drain of lactation, but the growing period was lengthened (McKenzie, 1928). A more recent study by Stewart (1945) showed that litter size increased with the age of the gilt from 9 months until 15 months but did not increase beyond this point. Under practical conditions swine are usually bred to farrow when from 12 to 14 months of age.

There is not complete agreement as to the influence of age on the fertility of dairy cattle, probably due to differences in cattle-management practices through the years and in different areas of the country, and in types of cattle observed. There is fairly general agreement that the breeding efficiency of heifers is lower than that of cows calving more than once and that fertility declines in animals more than 9 or 10 years old. A study at Cornell University involving 41 bulls and over 12,000 services to Holstein cows showed that the average breeding efficiency of all cows artificially inseminated was 48.2 per cent. It was maximum (50.6 per cent) in cows 4 to 6 years of age and minimum in cows 1 to 3 years of age or more than 10 years (46.5 per cent in both groups). In the bull, the only outstandingly high figure was 56.1 per cent breeding efficiency in the 2-year-old group and an average of 48.2 per cent in bulls ranging from 1 to 12 years of age (Tanabe and Salisbury, 1946). A study of breeding efficiency in the University of Nebraska herd between 1896 and 1934 showed that cows under 2 years of age were less fertile than cows from 2 to 10 years old and bulls under 2 years of age had the highest breeding efficiency (Morgan and Davis, 1938). A summary of the fertility of dairy bulls in the Purdue herd between 1920 and 1940 showed that bulls from 21 to 33 months of age had the highest efficiency (73.4 per cent), but a small number of 10- to 12-year-old bulls still had a breeding efficiency of 64 per cent. The data on older bulls are often biased because of

a tendency to eliminate older animals for many reasons other than lowered fertility and to retain some bulls of known lowered breeding efficiency but of outstanding blood lines.

It appears that the effects of age on the fertility of beef cattle are rather similar to those of dairy cattle. A study of about 1,300 Hereford cattle on the San Carlos Indian Reservation showed that when artificial insemination was used 2.37 inseminations per calf were required in animals 2 to 3 years old and only 1.36 inseminations per calf born in cattle 5 to 6 years of age. Fertility appeared to decline gradually after the sixth year (Lasley and Bogart, 1943).

Sheep are seasonal breeders and are ordinarily not mated until their second breeding season at 18 to 21 months of age. Ewes are well grown out by this time, and the age factor is of relatively little importance. However, Briggs (1936) showed that ewe lambs may be bred during their first breeding season when about 9 months of age. Such animals grew more slowly than those bred at their second breeding season but reached the same ultimate size. In general, there is an increase in lambing rate up to 3 to 6 years and a decline in lamb crop after this time (McKenzie and Terrill, 1937). It has been shown that lambs and yearlings have shorter estrual periods and a lower ovulation rate than mature ewes.

In the mare, breeding efficiency is lowest in animals entering the breeding herd for the first time and in mares bred at foal heat. Mares which are well grown out can be bred at 2 years of age, but most animals are 30 to 36 months of age before being placed in the breeding herd (Andrews and McKenzie, 1941).

Failure of females to reach their expected mature size is frequently attributed to the premature establishment of pregnancy. This excuse is invariably given as an explanation for the lack of size of a particular individual in a herd. The data which are available for farm animals indicate that lactation places greater demands upon an animal than pregnancy. If pregnant and lactating animals are *properly fed*, their ultimate size appears to be unaffected, even though the rate of growth may be reduced. This general problem has been extensively studied in rats at Cornell University, and although there are certain dangers in interpreting rat data in terms of farm animals, the results are of considerable interest.

It has been shown (1) that castrated female rats grew faster than bred or virgin rats; (2) that rats bred at normal age and their young killed immediately so that they were pregnant most of the time but not lactating grew more rapidly and for a much longer time than virgins or those bred early or late; (3) that early-bred and lactating females were somewhat retarded in growth due to lactation but that they eventually reached the

same adult size as those bred later; (4) rats bred at normal age (about 100 days and somewhat after puberty) grew most rapidly next to the castrates and those bred at normal age with young killed, and eventually reached the greatest weight; (5) that rats bred late were retarded in growth and did not reach the weights attained by castrates, those bred early, or at the normal time; (6) that virgin rats were most retarded in growth and attained the smallest size at maturity (Bogart *et al.*, 1940).

From the standpoint of reproductive efficiency it appears that early and regular reproduction is a stimulus to reproduction. Rats which were never bred showed irregularities and cessation of estrual cycles earlier than any of the mated groups. It was suggested that breeding promotes a greater harmony between the gonads and the other endocrine glands (Asdell *et al.*, 1941).

Relation of Breeding and Time of Ovulation.—As previously stressed, the chief objective of the livestock breeder is to time the breeding act in such a way that large numbers of viable spermatozoa will be present in the female genitalia at the time of ovulation. Such planned mating should be regarded as essential in the mare, since breeding within the first few hours of heat is almost certain to result in a sterile mating. At the other extreme is the chicken; in this species one natural or artificial insemination results in approximately 90 per cent fertility for an entire week.

In order that breeding and ovulation may be timed, it is assumed that the ovulation time of the species is known. In sheep the problem appears to be less acute than in the other farm animals. The heat period is relatively short, ovulation occurs near the end of estrus, and rams running with ewes usually mate more than once during heat.

Trimberger and Davis (1943) have shown that in dairy-cattle, breeding at the start of estrus results in much lower efficiency than at the middle of heat and that if insemination is carried out 12 hours or more after the end of heat, the conception rate is low. The fact that some cows conceived when bred as late as 36 hours after the end of heat probably indicated that these animals ovulated later than the average cow.

Practical recommendations for the various species will be made in a subsequent section.

BREEDING MANAGEMENT OF THE MALE

Service for Immature Males.—Although many studies have been made of the testicular development of males of various species, and the influence of such factors as age, nutrition, and season upon semen quality, little reliable information is available as to the optimum rate of use of males during the transitional period from puberty until somatic maturity has

TABLE 12.—BREEDING RESULTS IN FEMALES BRED EXPERIMENTALLY AT VARIOUS STAGES OF ESTRUS AND IN FEMALES BRED ARTIFICIALLY IN THE UNIVERSITY HERD*

Time of service	Number of cows bred	Cows conceiving from one service	
		No.	%
Start of estrus	25	11	44.00
Middle of estrus	40	33	82.50
Bred at middle of estrus and rebred in 24 hours	25	21	84.00
End of estrus	40	30	75.00
Artificial routine breeding	194	123	63.40
6 hours after estrus ended	40	25	62.50
12 hours after estrus ended	25	8	32.00
18 hours after estrus ended	25	7	28.00
24 hours after estrus ended	25	3	12.00
36 hours after estrus ended	25	2	8.00
48 hours after estrus ended	25	0	0.00

* Trimberger and Davis, 1943.

been reached. The data which are available seem to suggest that the ram and bull, species characterized by relatively small semen volume and high sperm concentration, can be used relatively frequently without evidence of permanent damage to reproductive performance. In the stallion and boar, species characterized by large semen volume and low sperm concentration, frequent use is followed by easily recognized deleterious changes in semen quality. In the absence of clear-cut experimental evidence, the authors draw on their own experience and that of practical livestock breeders in order that some concrete suggestions may be made. To err is human, and in this case the writers have attempted to recommend conservatively.

As previously stressed, there can be no substitute for the understanding of each sire's individual capabilities. In the farm animals sperm are produced in limited numbers long before skeletal and muscular growth are completed. It stands to reason that a certain degree of size must be attained before copulation can be performed with physical safety. The breeding habits of males should be *established,* not allowed to develop in a hit-or-miss fashion. The frustration of immature males in unsuccessfully attempting to serve animals which are too large, which are improperly restrained or in an unsuitable location, may have a lasting effect on the mental attitude of the sire. Males which fall because of slippery footing or receive head injuries because of use in low-ceilinged barns may be both physically and psychologically injured. The first practical suggestion, then, is that no male be used for service unless he is mated with a

physically suited female. Second, the sire must exhibit sufficient sex drive to complete the sexual act. Some males develop slowly in this respect, and others are apt to be restrained in the presence of man. Impatience and punishment at this time have no place in the intelligent breeding program. It is our opinion that care in the establishment of good breeding habits is just as important as the initiation of a heifer to the milking parlor or the high-strung Thoroughbred to the saddle.

If a sire is willing and able to give service, if these abilities are maintained following such use, and if the percentage of females which conceive is approximately the average breeding efficiency of the species, it would seem as though the male were being wisely used.

Bulls.—Widespread experience in artificial-breeding associations indicates that the *average* mature bull can be used at weekly intervals practically indefinitely without affecting semen quality. In most cases two successive ejaculations are obtained at each weekly collection period. During the early use of artificial insemination some bulls remained in useful service when ejaculated on alternate days or even every day, but such rate of service is now considered undesirable. Under natural breeding conditions a well-developed yearling bull can be expected to serve at least 25 cows between his first and second years. It would seem wise to distribute these services throughout the year, or at least not to concentrate several services per week into a short breeding season. Evidences of a decline in sex drive or loss of weight should be considered warning that the system of management is unsatisfactory. In view of the data showing that maximum fertility is usually attained at two years of age in bulls, it seems logical to expect animals to be capable of natural service at least once a week after this time. It is well known that bulls can be used two or three times daily without affecting fertility if they are allowed several days of sexual rest afterward. Many laboratory tests of the effects of repeated ejaculation on semen quality have been made. In one such test 24 ejaculations were obtained during a 27-hour period. The concentration of sperm remained constant until the fifteenth mating, after which it fell sharply. However, after an 18-hour rest sperm concentration rose to a high level again (Anderson, 1945). Many bulls have been ejaculated at intervals of 3 or 4 days for periods of a year with no observed harmful effects. Other bulls, which have given excellent results when used in natural service in small herds, have proven worthless when attempts have been made to collect at weekly intervals for artificial insemination.

Rams.—Under practical conditions, ram lambs are not ordinarily used until they are about eighteen months of age. However, lambs are capable of limited service during their first fall when about nine months old.

When the earliest possible progeny testing is of importance in genetic studies, a limited number of females can be mated to spring rams. In such cases, artificial insemination has the advantage of extending the use of young sires far beyond their natural capabilities.

It has been found very difficult to exhaust the sperm stores of mature rams. In one exhaustion test a particular ram after 42 consecutive ejaculations within a 9-hour period still ejaculated 100 million sperm (Anderson, 1945). Studies at the Missouri Station showed that there are wide individual differences in the semen production of rams, that complete sperm exhaustion is difficult to obtain, and that when the sperm are depleted, a short rest period is sufficient for restoration (McKenzie and Berliner, 1937). At two and one-half years of age a ram should be capable of serving 40 or 50 females, and older rams have frequently produced satisfactory results when mated with 80 or 90 ewes annually.

Boars.—There appears to be a discrepancy between laboratory studies on semen production of the boar and the breeding practices used by successful swine producers. McKenzie *et al.* (1938) showed that when boars were ejaculated at intervals of 24 hours or less, semen volume, sperm concentration and total numbers, and duration of sperm motility all declined. Two of three boars used at 12-hour intervals temporarily refused to mate after three or four services. Russian workers concluded that boars should not be used more than twice, and preferably once, in 24 hours. Yearling boars, it was reported, should not be used oftener than every other day if they are to be used for as long as 2 weeks (Anderson, 1945). An Indiana survey by Smith (1937) showed that swine breeders were agreed that mature boars can serve two or occasionally three sows daily. Nearly all the producers questioned reported that yearling boars could be used as frequently as older males without affecting breeding efficiency. Personal questioning of successful swine breeders by the author during the past 5 years has revealed that as many as four or five sows have been bred to one boar on a particular day without affecting fertility or litter size.

It is felt that some reservations need to be made in regard to the frequency of use of boars. The incidence of 10 to 20 per cent of non-pregnant sows in otherwise successful swine herds and the frequent occurrence of litters of two to four pigs cannot but raise the question as to the role of the boar in this problem. Current studies at the Indiana, Illinois, Missouri, and Wisconsin stations have shown that many sows which failed to conceive following repeated services on farms have become pregnant on the first service when taken to the experiment stations mentioned. It cannot be concluded at present that this is attributable to the boar, but it does suggest that the optimum use of

boars may fall somewhere between the recommendations of the research worker and the swine producer.

Stallions.—There are wide individual and breed differences between stallions in age at sexual maturity and in sexual capacity. In general, stallions should not be used until they are two years of age, and one service per week during the breeding season is usually not excessive. Stallions three or more years of age can be used more heavily. Here again, there is a difference of opinion in the optimum rate of use. It seems evident, on the basis of experience, that stallions can occasionally give up to four or five services per day, provided sexual rest is given after such use. In the authors' experience, mature stallions can be

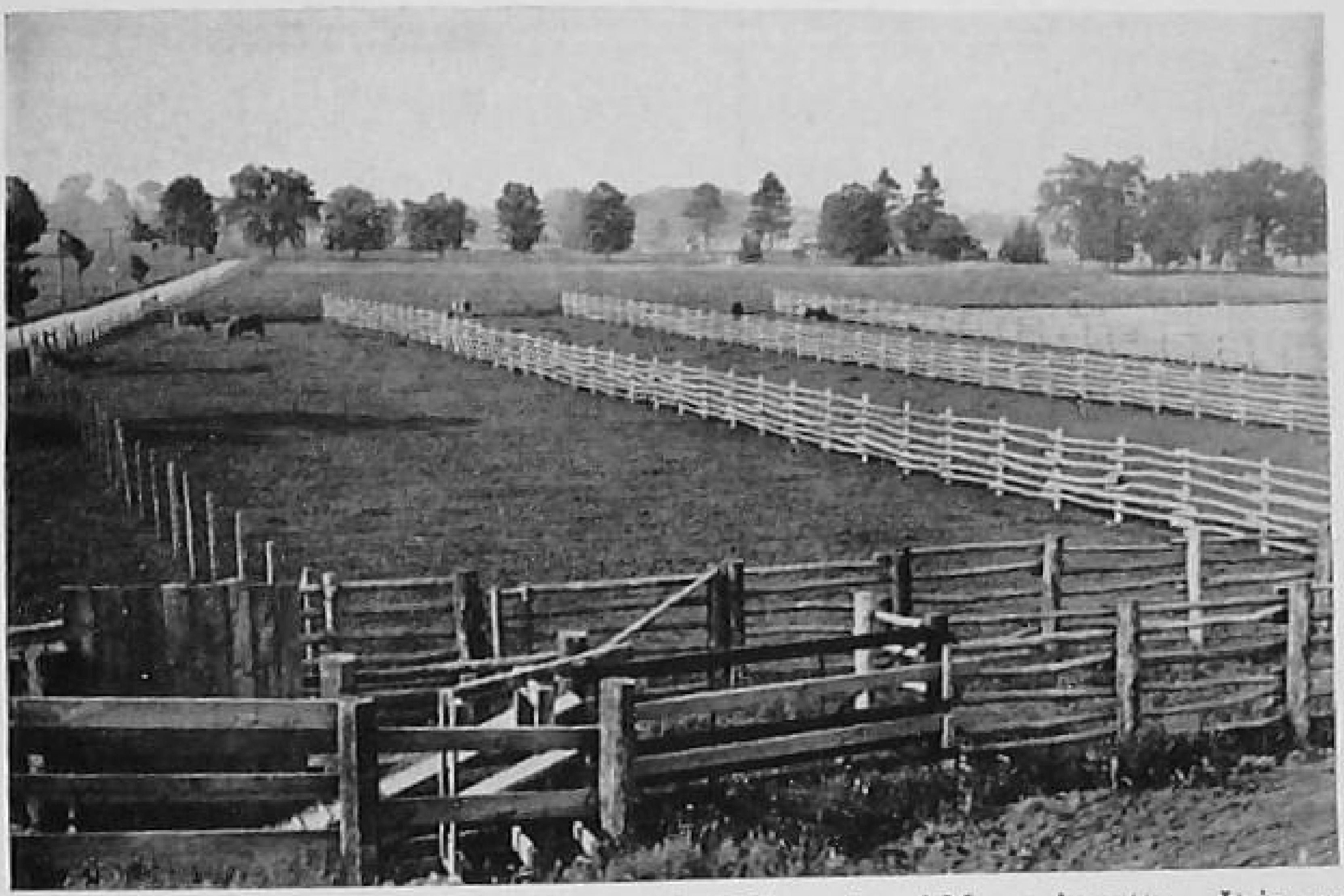

FIG. 60.—Exercising paddocks for bulls at the University of Massachusetts. It is essential that old bulls secure sufficient exercise.

expected to give six or seven services per week during a breeding season of 45 days without affecting breeding efficiency. Other workers have found that some stallions can be used twice daily for extended periods without harmful effects (Anderson, 1945).

General Management of Males.—Because the maintenance of maximum breeding efficiency of the male, from a purely physiological standpoint, to say nothing of his influence from a genetic standpoint, can and does contribute so much to the economic welfare of his owner, it would seem that the question merits a lot more attention than it often gets. The male is often kept in that part of the barn that does not lend itself to any other use or in some place on the farm where he will not interfere with other livestock operations. This location may vary, in the case of the bull, from a stanchion at the end of the barn, an abandoned

horse stall, or a muddy triangle between the barn and the silo. Bulls all too frequently receive the hay which the cows have previously sorted over and have no access to pasture or any source of green feed.

We will subsequently discuss the nutritional requirements for reproduction but will make no recommendations of specific rations for males. By way of summary, our present state of knowledge suggests that the quantitative and qualitative requirements for reproduction do not exceed those for the growth of young animals or for the maintenance of older animals in a state of good health. It should be obvious that the ration should contain a balance of carbohydrates, proteins, and minerals, and should supply the vitamins known to be essential for the various classes of livestock. The value of good pasture for breeding animals cannot be overemphasized. It is all too true that the scrub bull allowed to run with the herd is often more fortunate in this respect than the valuable purebred sire confined to a small exercise lot. It has been known for many years that fat sires are often sexually indifferent and may, in addition, be of lowered fertility. It is still not clear whether the fatness is the cause of lowered fertility or whether decreased testicular function results in increased fat deposition. Regardless of the cause, there seems little to be gained by the maintenance of a high degree of finish in breeding animals and much to be lost. The degree of fatness is, in some cases, due to feeding and management practices. Confinement of the sire in close quarters and the liberal use of carbohydrates is almost certain to result in fat deposition. The occurrence of obesity in the human may sometimes be of endocrine origin, but the consensus of medical opinion is that the chief cause is overeating. In the case of farm animals we can frequently attribute it to overfeeding.

The rapid development of artificial insemination has done much to focus our attention on the nature and causes of reproductive disturbances. Numerous attempts have been made to develop rations which will increase semen production and improve semen quality. As previously mentioned, it still appears that there are no special nutrients concerned only with fertility. Carbohydrate and fat deficiencies are extremely unlikely to occur in farm animals. The amount and quality of protein required by breeding males is still controversial. It has been reported that high protein intakes are both helpful and detrimental in bulls. Studies by Branton *et al.* (1947) have shown little difference in the fertility of bulls receiving 12, 16, and 20 per cent total protein. It has been reported that sources of animal protein such as skim milk, fish meal, and casein will improve fertility. Cornell experiments in which bulls were fed digestible nutrient levels of 100, 120, and 140 per cent of the Morrison dry-cow maintenance requirements showed no difference in fertility (Reid, 1949).

It is possible that specific nutrients or hormones or other chemical substances may eventually be found which will increase fertility beyond present levels, but until such substances are known, the emphasis should be on good feeding and management rather than on patented nostrums.

The exercise requirements of breeding animals is a favorite but controversial subject of livestock men. There is little disagreement that breeding males should be active, willing, and able to perform service quickly. The fat, sluggish male that will not perform service is a trial to even the most phlegmatic owner. The maintenance of animals in the desired state is most easily accomplished by providing large paddocks which contain good forage. In this way the animal receives valuable nutrients

FIG. 61.—A method for exercising bulls in use at experimental farm, Beltsville, Md. *(Courtesy of Bureau of Dairy Industries, U.S. Department of Agriculture.)*

and is provided an opportunity to exercise at will. Most animals can regulate their exercise needs. The amount necessary for one may be quite unsuited to another. A prominent and youthful university president has been quoted to the effect that whenever he feels the urge to exercise he lies down until it wears off. One of the most valuable results of a suitable paddock is the beneficial effect which it has on the health of the feet and legs. Animals which are confined in close, damp quarters may develop foot rot, overgrown hooves, and joint disturbances. It is tragic to observe a valuable and prepotent sire which cannot perform service because of feet and leg damage.

Numerous methods of forced exercise have been employed. There is little doubt that stallions are maintained in better general health and are more tractable when they perform regular work. This can be overdone.

Stallions have sometimes been given so much road work in an attempt to restore fertility that they have been physically exhausted. When large bull studs were first established for artificial insemination, all bulls, regardless of age, condition, or breed, were given a certain amount of exercise daily. It was soon observed that forced exercise could have undesirable as well as beneficial effects. There is no substitute for the recognition of individual requirements by an alert herdsman. There seems little wisdom in feeding large amounts of carbohydrates only to later walk them off on a treadmill, when the animal could better be maintained in a fit condition by judicious feeding.

Not a great deal is now known about equine, bovine, ovine, or porcine psychology. We have known for some time that certain animals did not mate readily, that moving sires to new locations was often followed by long or short periods of sterility. The underlying causes are not yet well understood, but they merit careful thought and experimentation. We have long known that males not trained to use a breeding rack in early life are often taught with great difficulty, if at all, in later life. Now, in artificial inseminating work, we are running into much the same problem of males refusing to serve while an attendant stands close by with an artificial vagina ready for use. Our highly bred animals are rather delicately balanced organisms from a nervous standpoint, and we have much to learn along these lines before we can get 100 per cent service (in the general sense of that term) from them.

Our males generally serve eagerly when young if conditions are made suitable. Our task is to retain that quality in them as long as we desire to use them. We know too, contrary to some rather extensive opinion, that genetically a male will transmit the same at any age—one or twenty—that the genes do not change with age, experience, production, or any other extraneous influences.

Males should be purchased subject to their ability, willingness, and success in impregnating sound, healthy females. It would probably be wise also before laying down a good price for a breeding male to have a veterinarian examine his semen, because what we are really buying when we purchase a male is semen containing viable germ cells, and these in turn contain, we hope, the genes that will bring about improvement in our herd or flock. For some types of genital diseases the only way to tell if a male is diseased is through using him. Preferably a male should be bred to a limited number of females and then held out of service for a few weeks to see if gestation is proceeding normally.

Besides making the external conditions conducive to the success of a young male's first service, strict attention should also be given to the internal conditions of the female genital tract. If, as should always be

the case, the young male has come from healthy parents, has grown up in a clean environment, and has been furnished suitable feed, he should reach puberty strong and uninfected. If this is true, one cannot be too careful in guarding him against infection. The male should be examined by a competent veterinarian and, if judged sound, he is ready for service. He should be allowed to serve only healthy females. The pernicious practice of allowing healthy young males to serve females that have been unable to conceive from one or several previous services cannot be condemned too severely, though it is often practiced, even when the female has a purulent discharge. Infection is all too prevalent and must be guarded against continually. A clean herd can be had if due care is exercised, and, when this end is once attained, its health should be guarded diligently in every detail.

Over a period of years your sires will make or break you, so select them intelligently and treat them understandingly.

BREEDING MANAGEMENT OF FEMALES

There is no single plan of breeding management for the various species of farm animals nor is there only one satisfactory system for each class of animals. In a nation as large and as diverse as the United States, to say nothing of conditions in other parts of the world, local conditions must be given primary consideration. The needs and the conditions of the professional dairymen supplying fluid milk for the New York City market are entirely different from those of the beef producer in eastern Montana. Calves dropped in January in a New York State barn have an excellent chance of survival, whereas in the northern range states calving must be confined to the spring months. For similarly good reasons, hand *vs.* herd or flock mating, artificial *vs.* natural service, lard type *vs.* bacon type, wool *vs.* mutton breeds are all questions which must be settled on their merits.

Cattle Problems.—Most cows come in heat at regular intervals throughout the entire year, but evidences of the seasonal breeding habits of primitive cattle still persist. In the larger dairy herds which are engaged in the production of milk for fluid consumption, breeding operations are ordinarily distributed throughout the year. In less intensive dairy areas and in the beef herds of the Western range states the breeding season is usually limited to the late spring and early summer months.

The average length of the entire estrual cycle is 19 to 20 days, and heat itself usually lasts 16 to 20 hours. In most cows ovulation occurs from 10 to 18 hours after the end of heat. An understanding of the estrual cycle of each cow is necessary if maximum breeding efficiency is to be attained.

When heat is first observed in the morning, it is recommended that service be given during the afternoon of the same day, since breeding in about the middle of the heat period has been shown to give optimum results. When it is known that estrus has begun in the afternoon, it is desirable to breed during the late evening, since the cow may be out of heat the next day. In such cows, if heat persists the following day, a second service on the second day may increase the conception rate.

The fact that cattle ovulate following the end of heat makes postestrual insemination possible. This has led some herdsmen to believe that cows can be inseminated at any time without respect to heat. This false impression can have adverse effects on breeding efficiency. If insemination is carried out within 6 hours after the end of heat, the chances of pregnancy are fairly good, although not so good as following service at mid-estrus. Under practical farm conditions there is nothing to be gained by two services in quick succession. There is some evidence that cows with exceptionally long heat periods or those in which ovulation may be delayed may benefit from two services at different times during heat. Natural service at mid-estrus followed by artificial insemination shortly after the end of heat may be helpful.

There are a few reproductive characteristics of cattle which differ from those of other animals. Cows have shorter heat periods than the other farm animals. It is easy, therefore, to fail to detect heat. When cattle appear to miss heat periods and have cycles of 38 to 42 days, there is a good chance that a heat period has occurred without detection. The importance of a system of regular observation and recording of the heat periods cannot be overemphasized. The fact that cattle ovulate after heat has ended also puts them in a separate class. Obviously not all cows ovulate at the same time with respect to the termination of estrus. Abnormal ovulation time may cause infertility in otherwise normal cows. As suggested, breeding more than once may be helpful in such animals. When unusual ovarian activity is suspected, a specially trained veterinarian can verify it by rectal examination.

The interval between calving and the first heat period and its significance should be understood. Beef cattle usually come in heat sooner than dairy cattle. The average interval for all cattle is from 40 to 60 days but may vary from 6 days to 6 months or longer. When heat periods have not been resumed within 80 or 90 days, an examination to determine the cause should be made. The manual removal of the corpus luteum, if this is the case, can be easily accomplished.

Cattle are subject to several reproductive disturbances. The freemartin condition is more or less unique in cattle; 90 per cent of the heifers born twin to a bull are sterile. For this reason, but not the only one,

twinning is not a desirable trait in cattle. The occurrence of nymphomania and cystic ovary is more common in cows than in other animals, although it does occur in mares. Cattle have a higher incidence of genital diseases than other farm animals. Brucellosis is a national problem, and trichomoniasis and infectious vaginitis can be troublesome when established. The occurrence of abortion or any abnormal genital discharge should be investigated at once.

Swine Problems.—Sows do come in heat throughout the year and there appear to be no seasonal limitations to fertility. However, when sows farrow at all months and pigs of all ages are present on individual farms, there are certain swine-disease problems which must be overcome. Sanitation must be given close attention and infectious diseases, such as hog cholera, dysentery, and gastroenteritis, must be guarded against.

In the corn belt, sows are usually bred to farrow twice a year, in the spring and fall. In areas where the one-litter system is practiced, most sows are bred for spring farrowing.

The average length of heat is 2 or 3 days, and sows usually have longer heat periods than gilts. However, heat may vary from 1 to 5 days, and it is desirable to know its onset and termination by trying the sows daily. The total length of the estrual cycle is about 21 days.

It has been commonly believed that ovulation usually occurs on the second day of heat. However, there is much to be known about the time of ovulation as well as its pattern, whether most of the ova are shed during a short interval, and what the range between the first and last ova is. The best information which is available seems to indicate that sows ovulate during the second day of heat. We have recommended, therefore, that gilts be bred early during the second day of heat and sows sometime during the second day. Here again, practical swine breeders have some difference of opinion as to breeding time, and many report that sows can be mated at any time during heat with equal success. As mentioned previously, the fact that swine have a much lower breeding efficiency than has been thought should be good reason for more care in breeding management. The occasional female that stays in heat only one day should obviously be mated early during that day. The sow which stays in heat three or four days will undoubtedly benefit from service on both the second and third days. When a gilt and a sow are to be bred to the same boar, and both come in heat at the same time, it would seem logical to breed the gilt on the morning of the second day and the sow during the afternoon. If it can be avoided, the boar should not be used for successive services only a few minutes apart.

It is well known that some sows come in heat a few days after farrowing, but are seldom mated at this time. The next heat period ordinarily

does not occur until 3 or 4 days after the pigs are weaned. However, sows which have small litters may exhibit estrus while lactating and if the pigs are not weaned at the usual time will eventually resume estrual cycles.

There has been some practical interest in the establishment of pregnancy in lactating sows. Experiments by Robeson at the Ohio Station in 1918 showed that the separation of the pigs from the sows for several nights, but letting them run together during the day, would induce heat. A more recent study by Cole and Hughes (1946) showed that the injection of 1,000 I.U. of equine gonadotropin between the thirty-ninth and sixty-eighth days of lactation would induce heat in 3 to 7 days. This method has practical applications, especially in causing animals which farrow late to come in heat and thus concentrate the next farrowing season in a shorter period of time.

Among the more important swine-breeding problems which need solution are the embryonic and fetal death losses and the high early post-natal deaths. The most conservative estimates indicate that at least 5 to 20 per cent of the fertilized ova fail to develop and that 10 to 30 per cent of the newborn pigs die within the first week of life. Brucellosis is the only specific genital disease of swine which is widespread. Its dangers to man and the economic losses which it causes in swine make it a serious threat to the swine industry. It can best be guarded against by the introduction of only tested stock from herds of known disease status.

Sheep Problems.—Sheep are peculiar in that they have as yet successfully resisted man's attempts to eliminate the seasonal breeding pattern. Most breeds of mutton sheep exhibit estrus from August through January. In the Midwest, maximum fertility is usually attained during late September, and Hampshires and Rambouillets tend to become pregnant a little sooner than Shropshires and Southdowns. In areas where hot-house lamb production is practiced, Dorset × Merino ewes have been popular because of their tendency to exhibit estrus during the summer.

Breeding practices in the range states vary with local conditions. In the Southwest and coast states ewes are frequently bred to drop their lambs from January through March. In colder areas most ewes are lambed in May. It is apparent that the breeding time is limited not only by the seasonal patterns of the sheep themselves but by economic and geographic considerations.

The desirability of twins may depend upon the nature of the sheep project. Single lambs are usually larger and grow more rapidly than twins, whereas twins which survive produce more lamb meat per ewe. Because of differences in vigor, many range producers prefer single lambs. As will be discussed, whether or not flushing affects the size of the

lamb crop, there are no disadvantages to improving the nutritional status of ewes prior to breeding. Excess fatness prior to lambing is to be avoided, but the ewes must be fed a well-balanced ration if pregnancy disease is to be avoided.

Ewes remain in heat about 30 hours and ovulate shortly before the end of heat. When hand mating is practiced, breeding during the latter part of heat is preferred. The majority of ewes are bred by rams running with the flock, and there is no doubt that this method produces entirely satisfactory results if the ram is of normal fertility. It is desirable that the wool in the tail region be clipped before breeding in order to facilitate mating. In farm flocks, painting the brisket of the ram with used motor oil to which a dye has been added will mark the ewes which are bred. In this way a fairly accurate breeding record can be kept. Also, in farm flocks, the ram is sometimes turned in with the ewes for only a few hours daily. In this way his energies can be conserved, and he can be fed separately if he is losing weight.

Genital diseases in sheep are rare, and there are few problems which cannot be overcome by the application of knowledge which is already at hand.

Horse Problems.—The decline in the use of the horse as a source of farm power has resulted in an almost complete lack of interest in horse breeding by farmers. At the present time specialized horse-breeding operations are carried on almost exclusively by the producers of saddle, running, and light-harness horses.

Although well-fed mares come in heat throughout the year, most mares are bred to foal in the spring. The relatively long heat period (4 to 6 days) of the average mare and the relatively short life of stallion spermatozoa poses a problem of timing which is greater than in any other farm animal.

The serious horse breeder will find it essential to try mares for the occurrence of estrus every day, or at least every other day, during breeding season. Mares which have been mated should be tried frequently and not just at the twenty-first day after breeding. As previously explained, the average interval between heat periods is 14 to 16 days, and the reoccurrence of heat is often missed because of poor timing.

The average mare ovulates 24 to 48 hours before the end of heat, but it is impossible to predict this in advance. It is therefore agreed that most mares should be bred more than once during heat if the rate of conception is to be improved. We believe that the *optimum* system is the natural or artificial insemination of each mare daily, beginning on the second day of heat and continuing until heat ends. Some successful breeders recommend breeding on the third, fourth, and fifth days of heat,

and others breed every other day, beginning on the third day of estrus. If only one mating is possible, the fourth day of heat is probably the best. When stallions traveled from farm to farm, mares were usually bred once without respect to the day of heat. Under these conditions it is not surprising that only 40 to 50 per cent of the females bred conceived.

The chief problem in practical horse breeding is, therefore, one of having copulation and ovulation coincide. It has been believed for centuries that the best time to breed mares is during foal heat on the ninth day after foaling. This concept is unsound, not only because all mares do not ovulate on this magic ninth day, but because there is good evidence that genital diseases may be spread by breeding too soon after foaling. It appears that navel ill in the foal may actually begin its development when mares are bred during foal heat. Data from various horse-breeding areas indicate that fewer mares conceive when bred at foal heat than if mating is delayed until the second estrus period after parturition.

Breeder and Veterinarian Relations.—There are three possible points of view concerning the relations between breeders and veterinarians. One of these is that the veterinarian should be called to take care of every departure from normality in animals as regards health (or accident), no matter how slight. The other extreme is that an experienced herdsman can entirely dispense with the services of veterinarians and diagnose and treat all health abnormalities in his herd or flock. The writers think that both extremes are wrong and that there is a middle ground, somewhat variable between individuals, which is better for all concerned. If a cow scratches her udder or steps on a teat or a colt cuts himself on a barbed-wire fence, an avenue of infection is opened up that may result harmfully or even fatally. If the damage is great enough to require surgery or suturing, by all means the veterinarian should be called. If it is not, the herdsman can dress the wound, keep it clean, and bring about healing.

If an animal loses its appetite and becomes nervous and feverish, it may be due to a more or less trivial digestive upset or to constipation, which a dose of salts or castor oil together with more careful feeding for a few days would correct. It might, on the other hand, be the beginning of an acute case of colic or the onset of some fatal disease, the symptoms of which are totally unknown to the herdsman, and in these latter cases it would have been much better to secure the services of the veterinarian as soon as the trouble was discovered.

Sometimes the male becomes a bit slow and uncertain in service, or the females do not conceive. The herdsman may change the ration, start to feed minerals or vitamins, or try this or that panacea suggested by

well-intentioned neighbors or friends. Perhaps the herdsman himself has had a bit of experience and training in massaging ovaries, breaking out cysts, and so on. Many herdsmen with training and experience can do these things and do them well. For many others no amount of available training or experience seems to suffice. They just don't have the knack. If you are in the first-mentioned class, you are fortunate, and you probably also have the good sense to be on your guard at all times and to call upon your veterinarian when things look as though they are beyond your own power to deal with successfully. If you are one who lacks the training, experience, or knack in handling such things, you will be well advised to call on your veterinarian as soon as you notice something abnormal. And you will be still better advised not to let neighbors or others probably no better fitted than yourself start prescribing for or "treating" your animals.

Likewise, the time of parturition is a critical one for both mother and offspring, and again many herdsmen are capable of straightening up a fetus and of helping the dam to make a safe delivery. Other herdsmen are more or less helpless at this time if things are not normal. The same parallel might be pointed out regarding difficulties and abnormalities following parturition.

The veterinarian is all too often put in a bad hole to start with by being called only after a case has gotten really serious or by having not only the original trouble to contend with but also having to straighten out as best he can the bungling attempts of some not-too-intelligent animal nurse or midwife. From a purely selfish financial standpoint, overlong delay in securing the help of the veterinarian is generally "penny-wise and pound-foolish." The first prerequisite for success in animal breeding is the general and the reproductive health of our animals.

The need for veterinary services is a variable thing on all farms, and its need arises earlier under this owner or manager than it does under that one. Probably every herd needs veterinary attention at times, and it is for each man to determine his own "when." The extent to which the owner or herdsman can take care of the simpler health cases of his animals also varies within rather wide limits, and each man must learn his own abilities and more especially his own limitations. A good veterinarian in any case is an invaluable help to herd health, and, because this influences productivity and profits to such a large extent, the breeder, for his own good, must study the problem and use veterinary services in such a manner as will return the greatest profit to him. It certainly does not pay to be penurious in this field. It certainly does not pay to use "quacks" of any description. It certainly does not pay to remain ignorant of our own capabilities and limitations to render aid to our

animals, and, finally, and most important, it does not pay to delay over-long in getting needed medical care for abnormal, sick, or injured animals. A good veterinarian is about the best and most valuable friend a good breeding establishment can have. He merits fairer treatment than has often been his lot in the past.

If a man is serving as herdsman or manager of a livestock-breeding farm, he will do well to arrive at a very definite understanding with the owner as to the procedure to be followed regarding the use of veterinary service. Are you as herdsman or manager expected to supply veterinary as well as animal-husbandry services? Few men are thoroughly trained in both fields, and the lack of training is almost sure to show up sooner or later and usually with some cost to the owner. Are you to provide what medical service you feel you are fitted to, and are you free to call on whatever veterinarian you wish to whenever you think you need his services? Are you to provide animal-husbandry services only and to notify the owner whenever you think veterinary services are called for? Is a veterinarian to be employed to make regular health examinations and to be entirely responsible for both the general and genital health of the herd or flock?

TABLE 13.—REPRODUCTIVE PHENOMENA

	Age at puberty, months	Normal breeding season	Age first bred	Length of heat period	Length of gestation period, days	Rebred after parturition
Horses..	10–12	April–July	3 years	5–6 days	336	24–30 days after foaling
Cattle..	4–8	Any time	15–30 months	16–20 hours	281	60–90 days
Sheep..	4–8	September–December	18 months	30 hours	147–152	Next fall
Swine..	3–7	December and June	9 months	2–3 days	112	3–5 days after weaning pigs

All these systems may work under certain circumstances, but there will be much less loss and misunderstanding if a general policy can be adopted and followed. If you are the owner of the animals, the decision as to health policy is yours and should be made, and, when made, adhered to.

The situations referred to are largely of an emergency nature. All livestock men should also inform themselves in regard to the symptoms, prevention, and control of diseases which affect the entire livestock industry. Such communicable diseases as tuberculosis, brucellosis, hog

cholera, mastitis, hoof-and-mouth disease, and several others are of national importance, and numerous local and national programs for the elimination of these diseases have been developed. Purebred breeders, particularly, should familiarize themselves with the rules and regulations in regard to livestock sales, exhibitions, and interstate shipments. The local veterinarian, the state veterinarian, and The Bureau of Animal Industry are all concerned with the preservation of our livestock in the best possible state of health, not only for economic livestock production but for the prevention of diseases of animals transmissible to man.

In recent years, in both human and animal medicine, there has been increased emphasis on the prevention or early diagnosis of disease and disorders. It is obviously more satisfactory to prevent such disturbances than to cure them, and it is likewise easier to correct them in their early stages than after they have become well established.

Many cattle breeders have adopted the practice of routine genital examinations of all breeding animals. The herd is usually visited at monthly intervals by a veterinarian who is especially trained for such work. Animals which have not resumed their estrual cycles at the expected time following calving are examined. The cause is often readily apparent and easily corrected, *e.g.*, a persistent corpus luteum. Cows with irregular heat periods, animals which have been bred repeatedly but have failed to conceive, and those with any evidence of abnormalities are carefully examined. Cows which have been bred and which have not returned in heat are examined to see if they are pregnant. All too often, animals which have not returned in heat are sold as nonbreeders only to be found gravid at the time of slaughter. The keeping of adequate records and the regular examination for pregnancy will eliminate such errors. In other cases, animals which have little or no likelihood of becoming pregnant are kept in herds in the hope that they will conceive. The elimination of such animals will save much time and expense. The detection of an infectious genital disease or other disturbances in their early stages may allow for easy correction and safeguard the other animals in the herd.

Summary.—In this chapter we have discussed the actual practice of breeding animals and have considered data on the breeding efficiency which can be expected in average disease-free animals. We have emphasized the fact that breeding efficiency can usually be increased by the intelligent application of knowledge which is available, but we have likewise pointed out that more knowledge is needed and that there are differences of opinion as to the effectiveness of certain practices. As discussed in the following chapter, there are numerous recognizable causes of lowered fertility and sterility. In this chapter we have tried to

account for the differences in the fertility of apparently normal animals. Species differences and the effects of age, sexual use, time of mating, and above all, the individual characteristics of animals, have been considered.

Reproductive efficiency can be maintained only by constant care in the selection, purchase, or sale of healthy animals and by managing them to the best of our ability and knowledge. Although it has not been proved to the satisfaction of scientists, there is much to support the idea that the breeding performance of the adult may be influenced by events during embryonic or prepubertal development. The task and problems of the livestock breeder are never ending and involve not just the animal but the soil, the crops, the seasons, and the microorganisms which influence all living material.

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CHAPTER VII

LOWERED FERTILITY AND STERILITY

For the breeder there is no more important economic problem than the fertility of his animals. Animals are simply natural machines that man has domesticated and improved for the purpose of turning feed into power, meat and/or milk, meat and wool, meat and/or eggs, or just meat alone; all these qualities except power and wool being dependent on fertility.

It is commonly believed that fertility and prolificacy are synonymous and are the exact opposites of sterility. This is not true. Whereas *sterility*, in a technical sense, means complete reproductive failure, the level of *fertility* may vary from 1 to 100 per cent. Since the labor, feed, and shelter costs of pregnant animals are but little more than in non-pregnant females, any reduction in fertility reduces the efficiency of livestock production. Breeding animals of the meat classes that do not bear young annually are clearly liabilities during such years. Dairy cattle that fail to conceive within 3 to 4 months following calving may be regarded as deficient not only in terms of offspring but in maximum milk production as well. The question of fertility is second to none in breeding. An animal's individual merit and genetic prepotency to stamp its good qualities on its offspring are without value if such animals leave few or no offspring.

Definitions.—*Fertility* denotes the ability of an animal to reproduce its kind. In animals characterized by sexual reproduction, fertility may be limited by either sex. The mating of a highly fertile male to an infertile female has the same result as the mating of two sterile animals. Any animal which has the ability to cause pregnancy or to become pregnant is, technically, a fertile individual. It is of great importance that the livestock breeder recognize that there are all degrees of fertility. All too frequently herd sires are purchased with a guarantee of fertility. Many such animals produce a few offspring, thus leaving the purchaser no recourse against the seller, but their degree of fertility is so low that they are economic liabilities as herd sires.

Sterility may be defined as complete reproductive failure. Such animals are easily recognized. It is frequently stated that a sterile sire is far less expensive than one of lowered fertility. This is true because the

failure to cause any conceptions is soon apparent and must be dealt with at once. The sire which settles an occasional female is often continued in service in the *hope* that he will soon improve. Such optimism may disrupt the entire breeding program and cause considerable financial loss.

Fecundity, meaning fertility or prolificacy in a general sense, comes from the same root as fetus, and for this reason its use is more or less restricted to females.

Prolificacy implies especially frequent or especially large numbers of offspring and is also more or less restricted in its application to the female. In all the higher species the production of young is contingent upon the

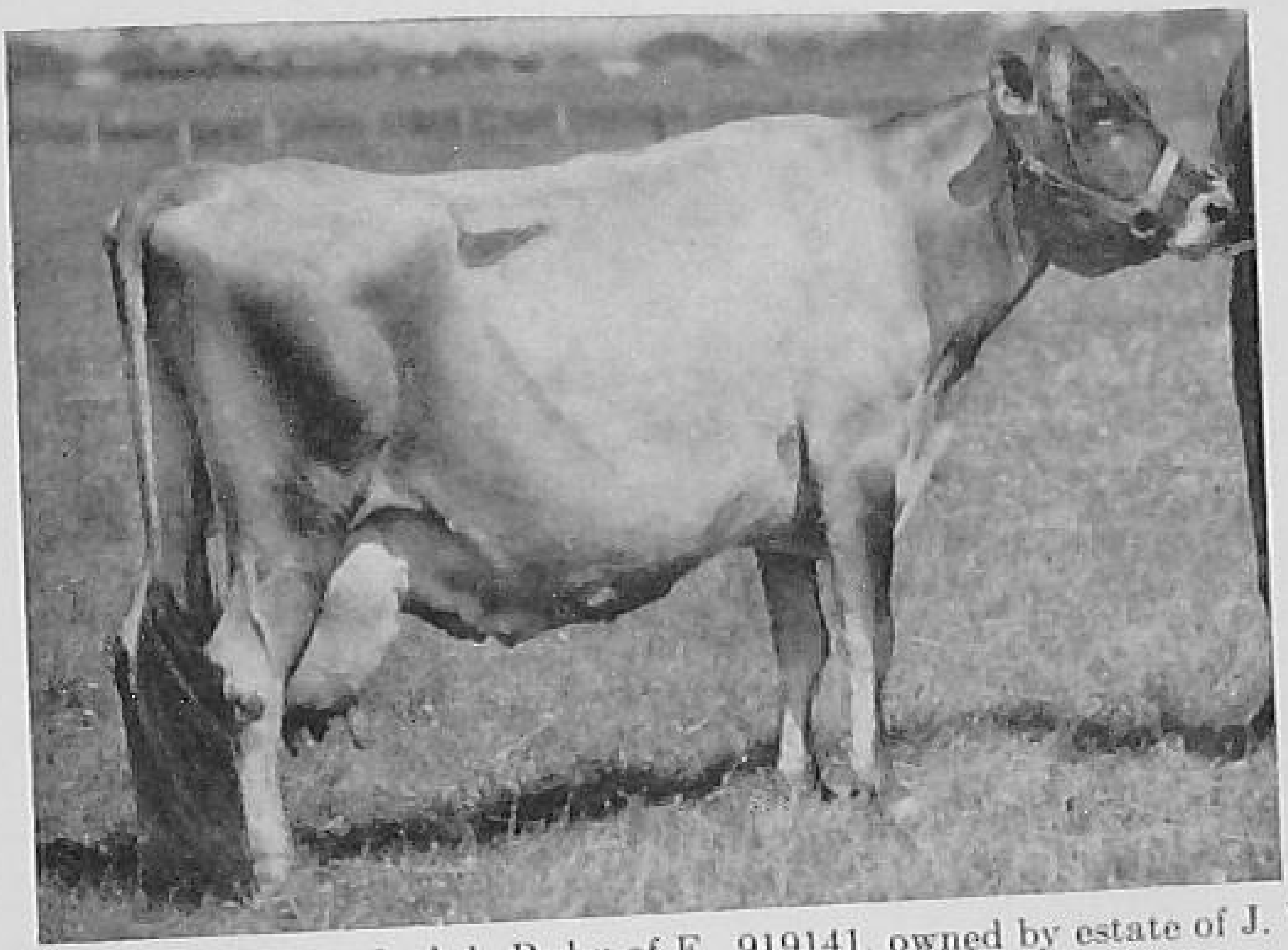
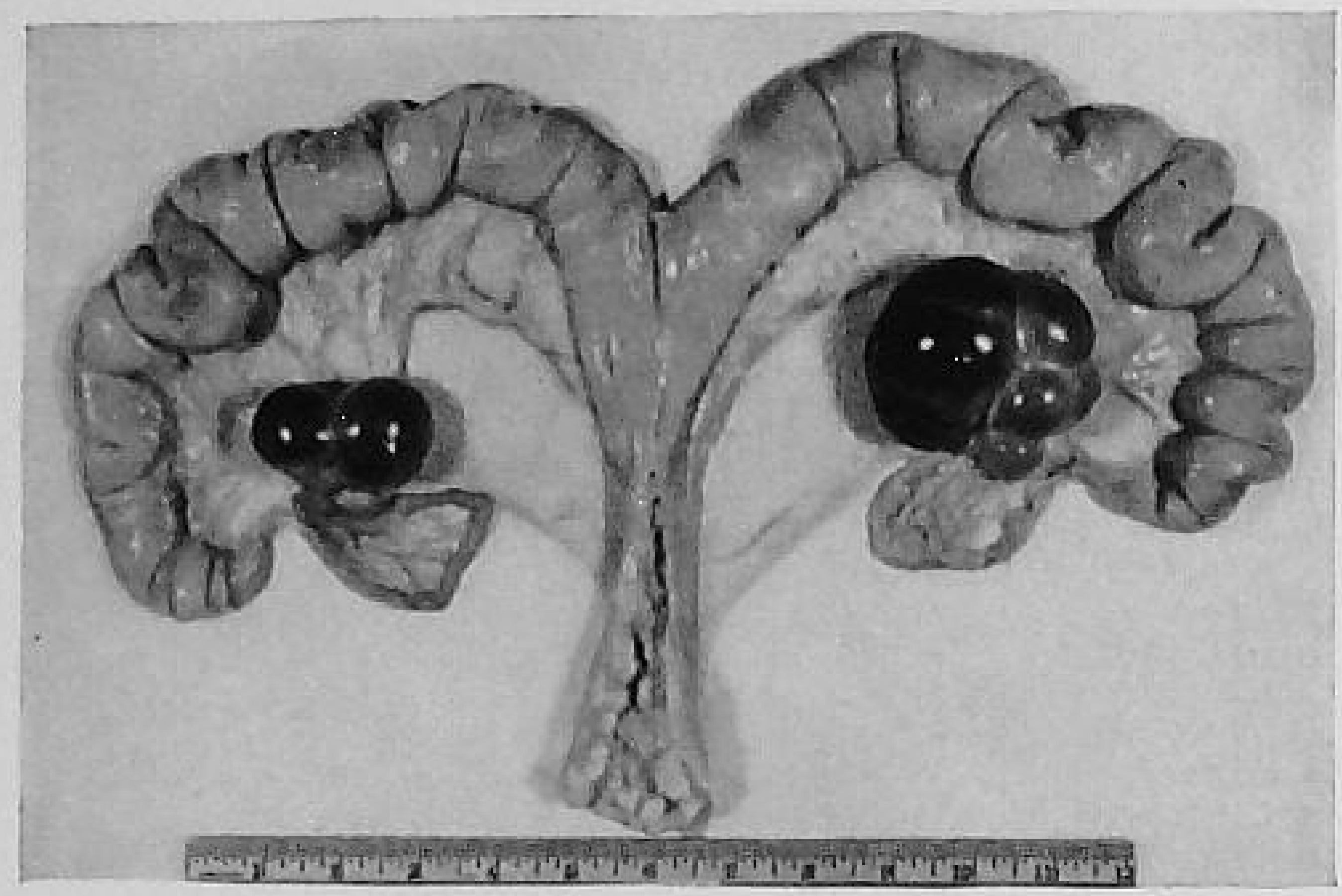


FIG. 62.—Jersey cow, Silken Lady's Ruby of F., 919141, owned by estate of J. W. Coppini, Ferndale, Calif. In September of 1949 this cow was nineteen years and four months old and had produced 181,977 lb. of milk, 10,048 lb. of butterfat, and 18 calves. (*Courtesy of American Jersey Cattle Club, photograph by Phil Palmer.*)

union of viable germ cells from both parents. In those species, however, which normally produce more than one offspring at a time, prolificacy is measured through the fecundity of the female, for the reason that a fertile male produces enough spermatozoa at a service to fertilize billions of ova. In swine the number of pigs per litter depends not primarily on the boar, provided he is producing viable spermatozoa, but upon the number of ova that have matured in the sow's ovaries. Likewise a ram, granted normal breeding health, cannot affect the number of twin or triplet births, for this depends on the number of ova produced by the ovaries of the ewe. Nevertheless, the inherited power to produce large litters in hogs or twins in sheep can be transmitted by the boar or ram to his offspring, and its effects make their appearance in the second generation. For this reason, it is wise to select boars from large litters and rams from twins, other things being equal or being given due consider-

ation. In any case, males should be selected from naturally fertile strains, which can be determined, of course, only by complete records of the ancestors and collateral relatives.

Reproductive efficiency connotes the optimum effective use of the reproductive powers of all the animals in a herd or flock. In the female it is the regular production of offspring over a period of years; in the male it



1. Cystic ovaries.

2. Hydrosalpinx.

FIG. 63.—Female genital abnormalities in swine. Compare the size of the follicles with (2). Compare the enlarged Fallopian tubes with (1). (*Courtesy of Drs. Warnick, Grummer, and Casida, University of Wisconsin.*)

is the successful fertilization of the largest number of eggs with the fewest possible services. This problem will be dealt with in a separate chapter.

Causes of Reproductive Failure.—There is the common erroneous belief that sterility is a single problem, that it is a specific disease which can be corrected by the administration of certain drugs, the injection of specific hormones, or the addition of certain vitamins and minerals to the ration. No concept could be further from the truth. In some

instances a specific condition or a particular disease can be identified as the cause of reproductive failure. In other cases no apparent reason for sterility or lowered fertility can be ascertained. However, the causes of reproductive failure can most frequently be found among the following: (1) anatomical defects, (2) mechanical injury of the genitalia, (3) genital

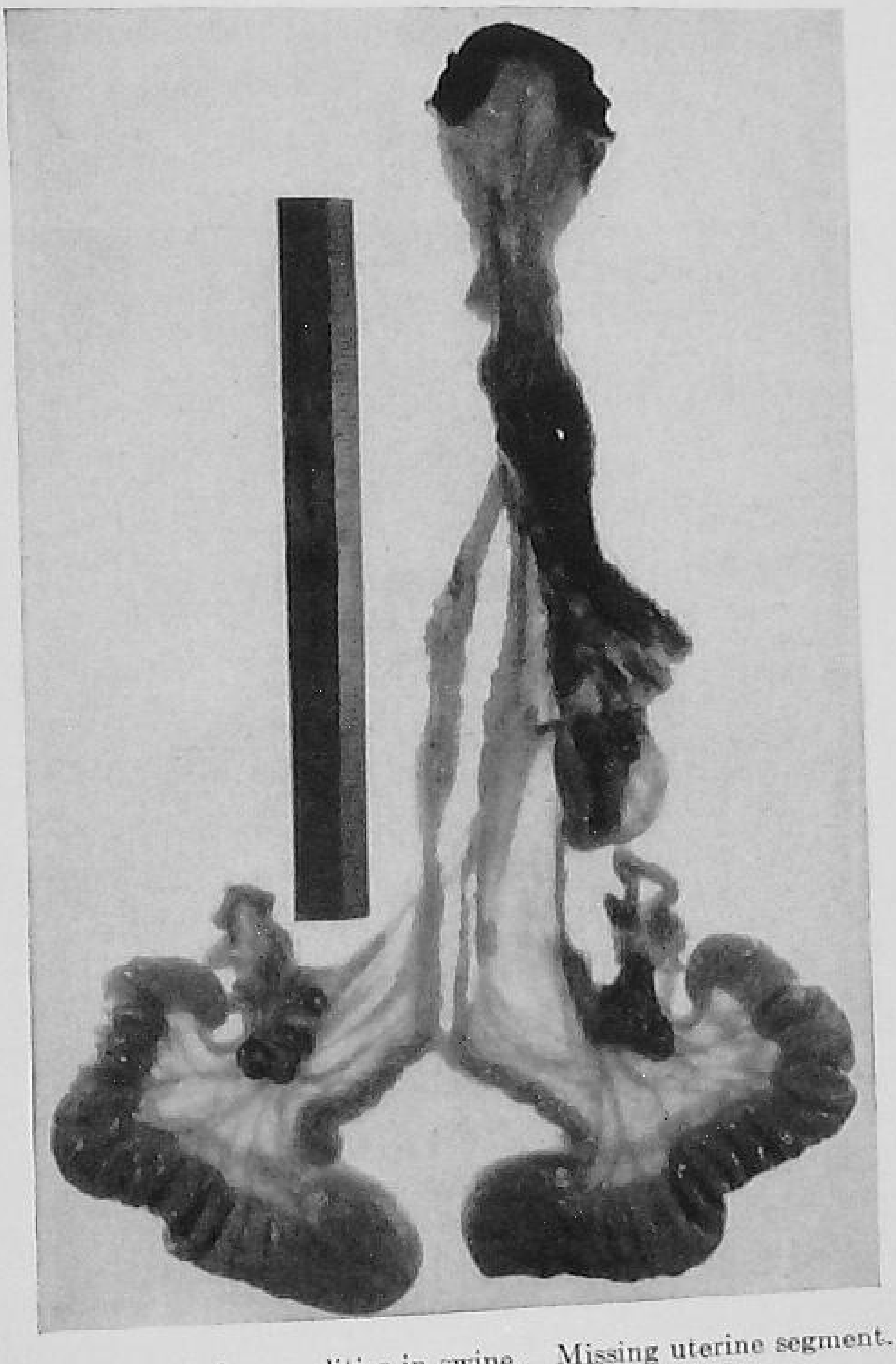


FIG. 64.—Female genital abnormalities in swine. Missing uterine segment. (*Courtesy of Drs. Warnick, Grummer, and Casida, University of Wisconsin.*)

diseases, (4) nutritional deficiencies, (5) genetic make-up, (6) physiological disturbances, and (7) miscellaneous environmental factors.

The reproductive processes may be interrupted in a wide variety of ways and at any stage. The causes range from the lack of sex drive and the unwillingness of animals to mate, the death of the gametes or the fertilized ovum, abortion, or the birth of a mature but dead fetus.

Anatomical Defects of the Genitalia.—Literally hundreds of types of anatomical defects of the genital organs have been reported. Some of

these are of sufficient severity as to cause sterility and others affect the degree of fertility. No attempt will be made to describe all the anomalies which have been reported in the literature, but to give a brief account of the more general types.

Probably the most common male genital defect is cryptorchism. This condition has been described in a previous chapter. The results of cryptorchism depend upon the exact location of the testes and vary from normal fertility in the unilateral cryptorchid to complete sterility when both testes are fully within the abdominal cavity. It is established that

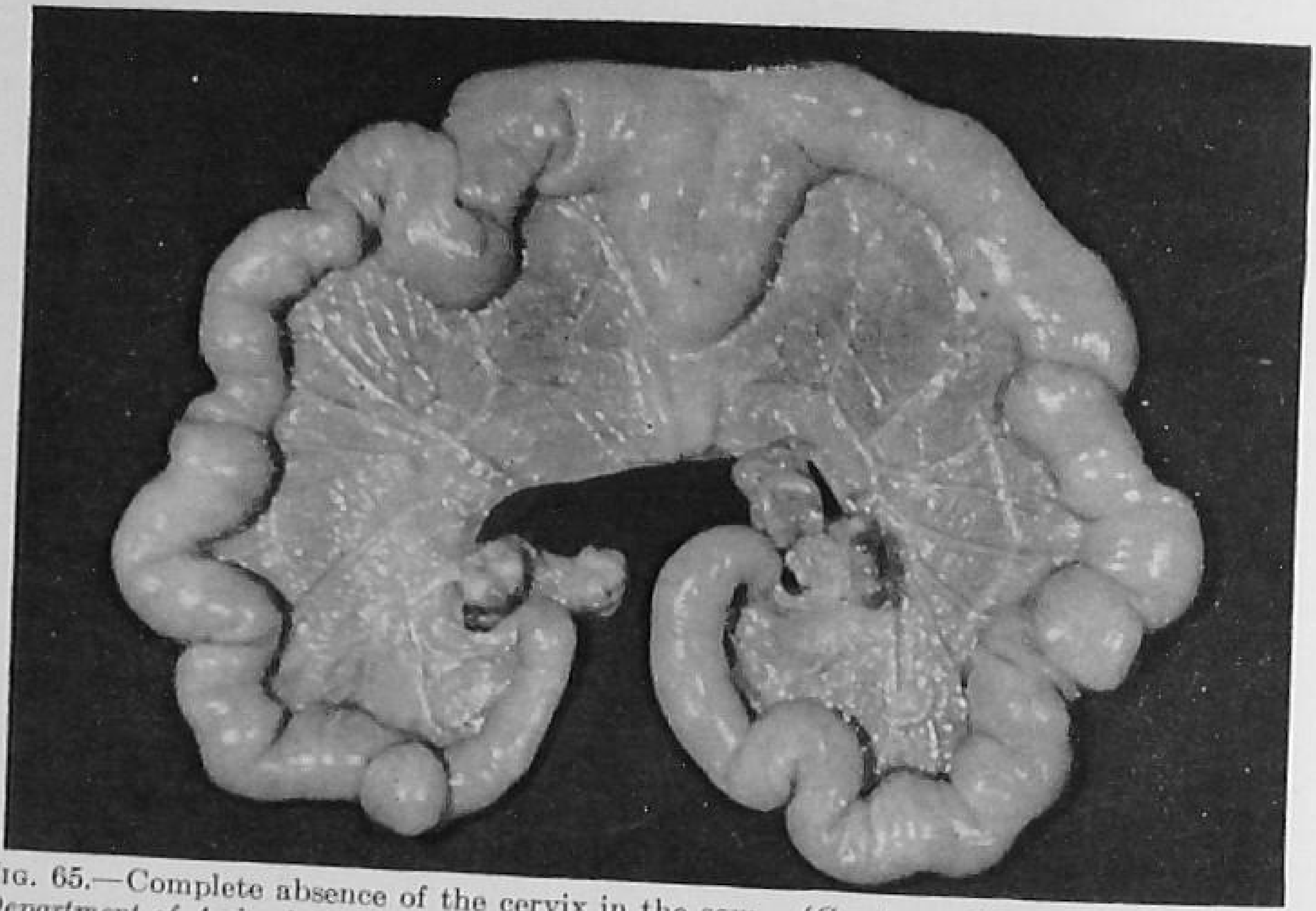


FIG. 65.—Complete absence of the cervix in the sow. (*Courtesy of Dr. A. V. Nalbandov, Department of Animal Science, University of Illinois.*)

the condition may be heritable and it should not be condoned in a breeding animal.

The occurrence of scrotal hernia is not uncommon. The descent of the viscera through the inguinal canal into the scrotum may interfere with the circulation of the testes and result in their atrophy. The development of a hernia in any part of the abdominal wall, although the testes may themselves be unaffected, may interfere with service and indirectly affect fertility.

The penis is sometimes malformed or may be prevented from full extension by adhesions within the sheath. Paralysis of the retractor muscles may allow the penis to protrude from the sheath and be subject to injury. Such defects may have no influence on the actual production

of sperm by the testes but may prevent effective service. The complete absence of portions of the genital system is rare, but does occur.

The general anatomic soundness of males, especially their feet and legs, should not be ignored. It is well known that broken limbs, sore, overgrown, or malformed feet, and arthritic joints may prevent males of normal fertility from mating.

Probably the best known anatomic abnormality in the female is the freemartin condition. Of all the farm animals, cattle appear to be unique in the occurrence of this abnormality. The freemartin, at birth, appears to be a normal female calf. However, the genital organs are very small and fail to develop as the animal grows. The vagina is usually smaller than normal and cannot be penetrated to the normal depth. The uterus does not develop, the ovaries are abnormal, and the general appearance of the animal is more like that of a steer than a female. Such animals are sterile. This condition appears in about 90 per cent of the females which are born twin to a bull calf. The most acceptable explanation for the condition is that it results from a hormonal imbalance in the female, presumably caused by the secretion of the male hormone by the testes of the twin male fetus. If the placentae of the two calves are fused and have a common blood supply, the female develops abnormally. If there is no fusion of the blood vessels, both animals develop normally.

The term *white heifer disease* has been widely used to describe abnormal genital development in white or nearly white cattle. This condition has been reported to consist of a persistent band of tissue which occludes the vaginal opening just anterior to the urethra. Such an obstruction obviously interferes with copulation. It has been shown that conception may follow surgical removal of the tissue. However, some clinicians use the term to describe abnormal genital structures in other than white cattle and abnormalities not limited to vaginal occlusion.

Many different anatomical abnormalities have been described in the female. Unilateral or bilateral absence of the ovaries, Fallopian tubes, or uterine horns occur in all species of farm animals. In cattle such abnormalities can be readily detected by a rectal examination. Fortunately, in both sexes, such abnormalities are not the most common cause of reproductive failure.

Mechanical Injury of the Genitalia.—From an anatomical standpoint the testes appear to be extremely vulnerable to injury; however, instances of bruising, inflammation, and lacerations of the scrotum and testes are not common. The consequences of such injuries vary from temporary reduction in fertility to complete sterility, and all injuries should receive prompt, expert treatment. The testes of the stallion are more likely to be injured during service than in the other farm animals. Mares which

are improperly handled or incorrectly restrained may permanently damage the testes or penis of the stallion.

The penis may become bruised or lacerated during service, thus resulting in temporary or permanent loss of the male as a sire. Most frequently such injuries could be avoided by the use of approved breeding practices or restraining devices.

A wide variety of injuries may occur in the female. The two critical times, as far as injuries are concerned, are parturition and service. As explained in an earlier chapter, complicated parturition may result in the loss of the offspring, permanent damage of the genitalia of the female,

FIG. 66.—University of Massachusetts Guernsey cow with her 1941 triplets, which followed sets of twins in 1938 and 1939. Two of these calves are bulls, one a heifer. What is the chance that this heifer will prove to be fertile?

or even death of the dam herself. Perforation of the uterine or vaginal walls, laceration of the cervix, eversion of the vagina, cervix, and uterus or of the rectum are all the sequelae of complicated birth. In some cases adhesions or secondary infections of the genitalia cause tissue damage which prevents further reproduction. Service by a large or vigorous male may cause permanent genital injury. Mechanical damage of the female genitalia due to other causes is rare.

Genital Diseases.—Theoretically, any disease which affects the well-being of an animal may have either temporary or permanent influence on fertility. In the male, for example, pneumonia, or any other disease accompanied by fever, may affect the rate of spermatogenesis. Severe

systemic infections may affect fertility or result in abortion in pregnant females. Conditions of this type are outside the scope of this discussion.

Of the farm animals, cattle are most likely to be affected by specific transmissible genital diseases. The economic losses suffered by cattle as the result of such diseases are probably many times greater than for all other farm animals combined. The authors will make no attempt to estimate the magnitude of such losses. The official U.S. Department of Agriculture estimate of losses attributable to brucellosis in cattle in 1942 was 30 million dollars (Mohler *et al.*). It has been estimated that in New York State alone the losses in cattle directly or indirectly due to breeding difficulties are 20 million dollars per year and seem to be increasing (Asdell, 1948).

Brucellosis.—Brucellosis of cattle (Bang's disease) is one of the major causes of loss in cattle production. This disease is caused by a specific organism, *Brucella abortus.* The brucella organisms ordinarily live in the pregnant uterus, but they may localize in other tissues such as the udder or in the testes. One of the most frequent, but not the only, evidence of infection is abortion. It is estimated that 85 per cent of abortions in cattle are due to brucellosis. Abortion may occur at any stage of pregnancy but it is most likely to occur between the fifth and eighth months. Aborted calves and the fetal membranes of brucella-infected cattle usually contain millions of the brucella organisms and the infection of other animals or the human may result from exposure to such material. Infected animals do not always abort, and their membranes may likewise contain the disease organism. The bacteria may be eliminated in the genital discharges for several weeks and have been known to be present in the milk for long periods of time.

Brucella infection may be introduced into or spread through a herd in several ways. Most frequently an outbreak follows the purchase of a supposedly healthy cow or the exposure of healthy cows to animals of unknown disease status at public sales and exhibitions or in community pastures. Brucellosis can be spread through contaminated feed, water, and bedding or directly from the body discharges of an infected animal of either sex.

One of the unfortunate misconceptions in regard to brucellosis is that abortion is the only sympton and the only cause of loss. Brucella infection does not result in complete immunity, but most cows abort only once following infection. The animals seem to develop a tolerance for the organism, although a few do abort twice and rarely three or more times. It has been estimated that 25 to 30 per cent of the cows which contract brucellosis may manifest breeding difficulties. This may be due

to various types of tissue damage in the genital organs. The fetal membranes are frequently retained following abortion.

Although many "treatments" for brucellosis have been proposed, research workers in this field know of no treatment which could be described as a "cure." The present (1949) method of control is based upon the detection of infected animals by testing the blood serum for the presence of agglutinins. This is accomplished by the addition of an antigen, prepared from *Brucella abortus* organisms, to measured amounts of cattle serum. Calves, even those born to infected dams, usually remain free of the disease if they are separated from infected animals and are not fed infected milk. It is believed that the vaccination of calves, when four to eight months of age, with a live vaccine prepared from a strain of *Brucella abortus* organisms of low virulence (strain 19) will confer sufficient immunity on such animals to protect them against subsequent exposure to brucellosis. Official plans for the elimination and prevention of brucellosis in cattle have been developed by most state livestock sanitary associations or the offices of the various state veterinarians. Recommendations are likewise available through the United States Livestock Sanitary Association and the Bureau of Animal Industry of the U.S. Department of Agriculture. Since no one plan is adaptable for all situations or each specific locality, it is recommended that the official agency responsible for the control of brucellosis in the area be contacted when the presence of this disease is suspected.

Brucellosis in swine is most often caused by *Brucella suis*. Swine are sometimes infected by *Brucella abortus*, and cattle may be affected by both the *abortus* and *suis Brucella*. Man may be affected by three types of *Brucella*, *abortus*, *suis*, and *melitensis*. The latter organism causes brucellosis in goats but rarely in cattle and swine and is not of much economic importance in the United States. Swine brucellosis is often a serious economic problem to the swine producer and may occasionally prevent the profitable operation of a swine enterprise (Hutchings, 1944). In cattle the presence of brucellosis in a herd is soon recognized by the occurrence of abortions. The incidence of abortions may vary greatly between swine herds, ranging from an occasional abortion to the majority of the pregnant females. In the boar the organisms may localize in the testis and produce a severe orchitis. Hutchings and Andrews (1946) have shown that brucella may be eliminated in large numbers in the semen, and it is well known that the boar is frequently a spreader of the disease. These bacteria may localize in the joints, causing arthritis; in the vertebral column, causing posterior paralysis; and abscess formation is not uncommon.

Abortion may occur at any time during gestation. This symptom has

been observed in experimental herds as early as 23 days after breeding. Under ordinary herd conditions such early abortions would probably not be detected, and this may account for the fact that the abortion rate sometimes *appears* to be very low. Swine usually abort only once, but as in cattle, such animals may be dangerous spreaders of the disease and their subsequent fertility may be affected.

The means of diagnosis of swine brucellosis is very similar to that of cattle. Satisfactory vaccination procedures for the prevention of the disease have not as yet been developed, and there is no known treatment. However, Hutchings (1947) has reported considerable success in the elimination of the disease from badly infected herds by the repeated blood testing of all swine and the isolation of negative pigs on clean premises as far removed as possible from the infected parent herd. The testing is begun when the pigs are weaned at *eight weeks* of age and is continued up to and during the first pregnancy. All reactors should be removed as they occur. The infected parent stock should be disposed of as soon as it is apparent that the younger animals are remaining free of the disease.

Bovine Venereal Trichomoniasis.—This disease is caused by a protozoon, *Trichomonas fetus.* Under natural conditions it is believed to be transmitted only by copulation, but it can be transmitted by infected instruments or in infected semen at the time of artificial insemination. The incidence of this disease and the losses which result from it are not so well known as in the case of brucellosis. Morgan (cited by Bartlett) reports that 61 infected herds were detected by the University of Wisconsin animal disease diagnostic laboratory between 1941 and 1946. Bartlett (1949) estimated that in nine trichomad-infected herds (more than 800 cattle) in the Beltsville, Md., area, the losses due to the infection were at least $200,000.

The damage which occurs following infection is confined primarily to the female. The organisms inhabit the uterus and bring about the early destruction of the embryo, usually within 3 to 5 weeks after conception. The animals then return in heat and may remain infected for several months. In some cases the uterus may become filled with pus and greatly enlarged. If such animals are not bred, they usually recover spontaneously, since the protozoa cannot persist permanently in the nonpregnant uterus. If noninfected bulls are used, the possibilities of eliminating the disease are good, but care must be exercised that the bulls do not become infected. The cattle must not be rebred until it is known that the organisms are no longer present.

In the bull the trichomonads inhabit the preputial membranes and glans penis. There is no outward sign of infection and the sperm are

unaffected. Unlike the female, the male remains permanently infected and may transmit the organisms at nearly every service. The detection of this disease in the bull requires the services of an expert, since the habits of *Trichomonas fetus* can best be described as "tricky." It is the opinion of most specialists in this field that infected bulls should be regarded as permanently infected and should be disposed of. Numerous types of treatment have been tried, and there is some experimental evidence that a satisfactory treatment may eventually be developed (Bartlett, 1949).

Vibrio fetus.—*Vibrio fetus* is recognized as one of the occasional causes of abortion in both cattle and sheep. In cattle, abortion due to this cause may occur at any stage of pregnancy but most frequently between the fourth and seventh months. The incidence of the disease, the per cent of infected animals which abort, and the exact manner of transmission of the disease are poorly understood (Bartlett, 1949). Abortion in any species should be regarded as a potentially serious problem. An attempt to determine the cause of each abortion should be made. If brucellosis, the most probable cause, can be eliminated, the possibilities that either *Trichomonas fetus* or *Vibrio fetus* might be involved should be investigated.

It should be recognized that abortion, like sterility, is only a symptom and that it can have many causes. Injury, failure of the corpus luteum function, nutritional deficiencies, embryological abnormalities, systemic infection, or any general physiologic imbalance may be followed by abortion.

Vaginitis.—This term, which refers to inflammation of the vagina, is in very general use, but there is a divergence of opinion as to the cause or causes and to the significance of the condition. It is believed that one type of venereal disease which occurs in cattle is due to a virus. This disease is called vesicular venereal disease and is supposedly rare in the United States but common in Europe. It is recognized at the beginning by small papules which form ulcers which in turn heal in about 2 weeks. Both males and females may be affected (Bartlett, 1949).

A second venereal disease which appears to be widespread is nodular venereal disease (granular or nodular vaginitis). Some lesions or supposed evidences of this disease can be found in nearly every cattle herd. In some cases the tissue changes are confined to the vulva and in other instances may involve the entire vagina. Varying degrees of inflammation of the mucous membrane may be present and small nodules may occur. Lesions may be present in virgin heifers and either open or pregnant cows (Bartlett, 1949). In some cases there is no apparent effect on fertility and in others natural service may not be followed by

pregnancy. In obviously infected herds where the conception rate was low following natural service, the use of artificial insemination has been reported to improve breeding efficiency. The explanation for this is apparently that the sperm are deposited in the cervix beyond the infected area. There is evidence that the infection (or some infections) may be spread by the bull, yet there is other evidence that the condition may not be primarily infectious.

Infectious Abortion in Mares.—Because of the decline in brood-mare numbers there is little current research on infectious genital diseases of the horse. Dimock and Edwards (1928) report that, in their experience, streptococcic abortion is most common in mares but that *Salmonella abortivo-equinus* and abortion due to a virus do occur.

Nutritional Deficiencies.—Few topics in livestock production have received so much attention as the influence of nutrition on reproduction. Since growth and reproduction are the two most fundamental characteristics of animals and since both are easily measured, it is not surprising that both are included in the design of the majority of nutritional investigations. There is hardly a nutritional substance or element that has not at one time been thought to be essential for normal fertility. It is self-evident that maximum reproductive efficiency depends upon the maintenance of a reasonable state of body health. It is likewise understandable that the absence of an essential nutrient may indirectly affect reproduction. In the case of a nutritional anemia, for example, the severity of the anemia may cause general debilitation and weaken the individual to the point where mating does not occur. It is entirely possible that fertile ova or sperm might be produced but that reproduction might be physically limited.

It is well known that the general plane of nutrition may affect fertility. In the rat it has been shown that a decrease of about 30 per cent in energy intake will affect fertility and that a marked retardation in the growth of the immature rat or a loss of weight in the mature animal may reduce or prevent gametogenesis in both sexes (Friedman and Turner, 1939). It has been observed, although not corroborated by experimentation, that both human and animal fertility is lowered following prolonged drought, famine, or war.

There is the general belief among livestock men that both extreme undernutrition or a very high plane of nutrition are equally harmful. It is commonly said that a particular animal is sterile because it is extremely fat. This problem should be considered from several points of view. From the physiological standpoint, it is well known that a reduction in the production of the sex hormones is followed by increased fat deposition. This is the basis for the practice of castration. It is logical, therefore, to

consider the possibilty that some animals which become excessively fat on the same ration which produces satisfactory results in the rest of the herd are fat because they are sterile, not sterile because they are fat. From the nutritional standpoint, a ration which is conducive to fat deposition may be quite unsatisfactory from the reproductive standpoint. The requirements for fattening are more easily met than are those of growth, reproduction, and lactation. A ration high in carbohydrates may produce excellent fattening but may not meet the requirements for optimum fertility. For this reason the selection of breeding animals from the fattening pens is subject to criticism.

Probably the best known of all feeding practices in relation to breeding management is flushing. It has long been an accepted practice to increase the plane of nutrition of breeding ewes prior to actual mating. This can be accomplished in a variety of ways such as the use of lush pastures and/or protein, carbohydrate, or vitamin supplementation. It seems to be accepted as the result of experiments in several countries, that flushing results in a larger lamb crop, although estrus is not induced earlier than usual (Friedman and Turner, 1939). Yet, when ewes have previously been maintained on a high plane of nutrition, flushing appears to have no beneficial reproductive effects. An 8-year study at the Oklahoma Station by Briggs *et al.* (1942) showed that, under the conditions of the experiment, flushing did not increase the number of lambs dropped and that the cost of the increased feed used during the breeding season was not justified by an increase in lamb crop.

When a flock of purebred range ewes which had produced an 80 to 100 per cent lamb crop under range conditions was transferred to the California Experiment Station, the lamb crop during the next 6 years averaged 135 per cent and reached a high of 160 per cent. It appears that improved feeding and management can markedly affect fertility under some conditions (Hart and Miller, 1937).

At the Utah Station Esplin *et al.* (1940) found that differences in the fertility of sheep were related to plane of nutrition during the lamb's first winter. Ewe lambs fed supplemental feeds gained about 25 lb. from October to April, whereas comparable ewe lambs on range gained 10 lb. Both groups were on the same range from April until the following October at which time they were placed in the breeding flock. At breeding time the lambs which received supplementary feed during the first winter weighed only 2 to 3 lb. more than the others. The lambing results of the two groups were quite different. Only 45 per cent of the "range" lambs produced offspring, whereas 65 per cent of the "fed" lambs reproduced. It was concluded that the nutritional regime during the growth period may subsequently influence reproductive capacity.

Studies at the Massachusetts Station clearly showed that the testicular development of boars was retarded when the plane of nutrition was sufficiently reduced to limit growth rate.

A comprehensive review of nutrition and sterility in dairy cattle by Asdell (1949) cites over 50 references on cattle alone.

Nearly every vitamin or special dietary factor has been suspected of limiting reproduction. In the farm animals, with the exception of the chicken, vitamin supplementation has been chiefly confined to vitamins A and D. While vitamin D can limit skeletal growth and general health,

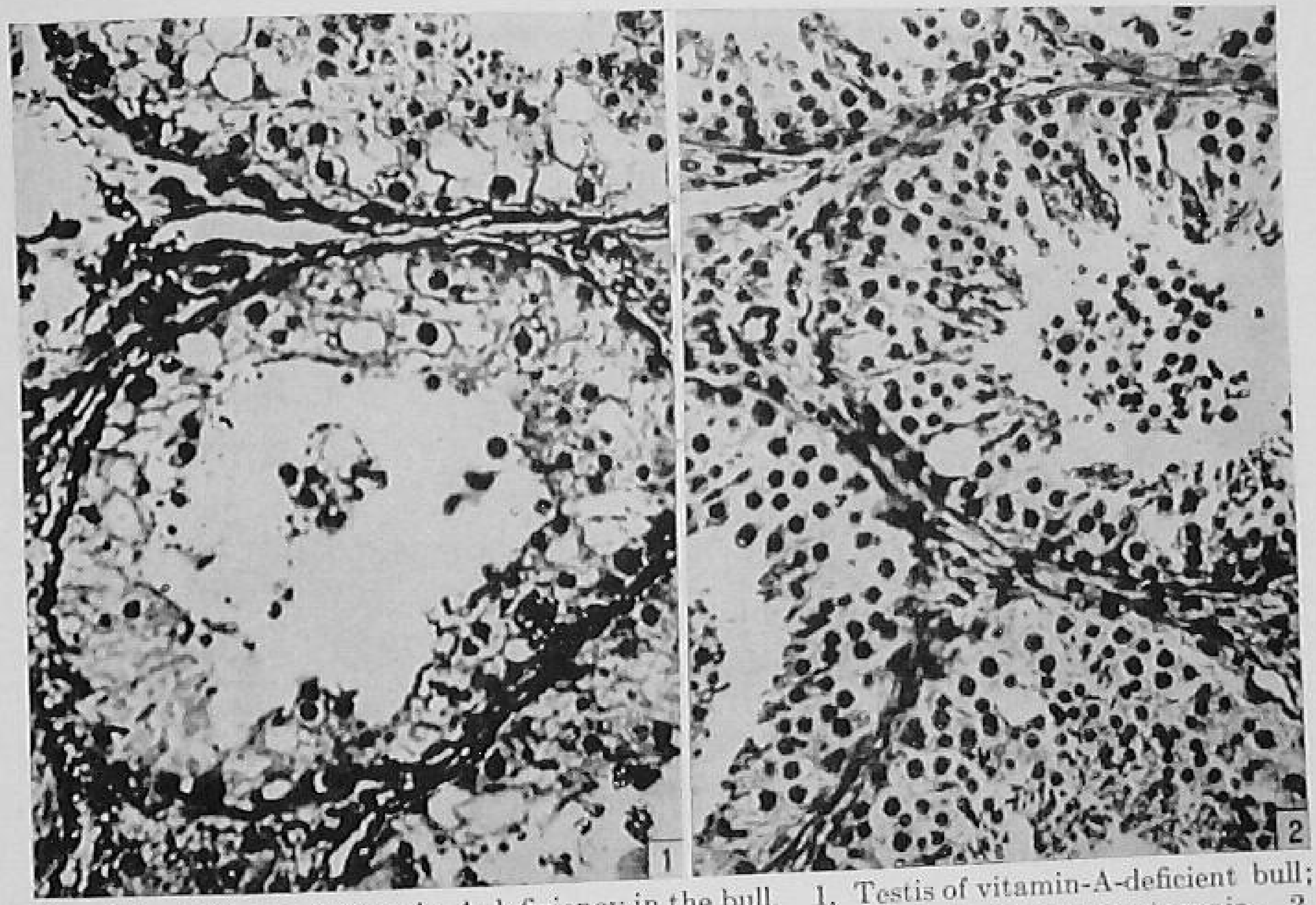


Fig. 67.—Effects of vitamin-A deficiency in the bull. 1. Testis of vitamin-A-deficient bull; observe absence of sperm and scarcity of all epithelial cells including spermatogonia. 2. Same bull after 4 months of vitamin-A therapy, extensive but not complete repair.

it has no direct effect on the genitalia. Vitamin A, however, is essential for normal reproduction. Under natural conditions vitamin A deficiency is likely to occur in animals which have been on dry feed, poor roughage, or drought-stricken range for extended periods of time. Under such conditions systemic evidences of vitamin A deficiency are usually recognizable. Night blindness, ophthalmia, diarrhea, and difficulties in locomotion and coordination may occur. In the male the rate of spermatogenesis and quality of the semen declines. In advanced stages of the deficiency the male may be unwilling or unable to copulate, even though motile sperm may be present. The cause of impaired fertility in the male is usually attributable to testicular damage. In the female conception may occur but is frequently followed by abortion, the birth of

dead or weak calves, and retention of the fetal membranes. Some workers report that vitamin-A deficient cows do not conceive so readily as normal animals (Asdell, 1949).

Several recent studies have been made of the effects of vitamin-A deficiency in bulls. In the young male the absence of vitamin A prevents both normal growth and normal testis development. Fluid-filled cysts may occur in the pituitary gland and complete reproductive failure can be expected. In sexually mature bulls vitamin-A deficiency produces varying degrees of testis degeneration and general debility, depending on the degree of the deficiency. In older animals the damage can usually

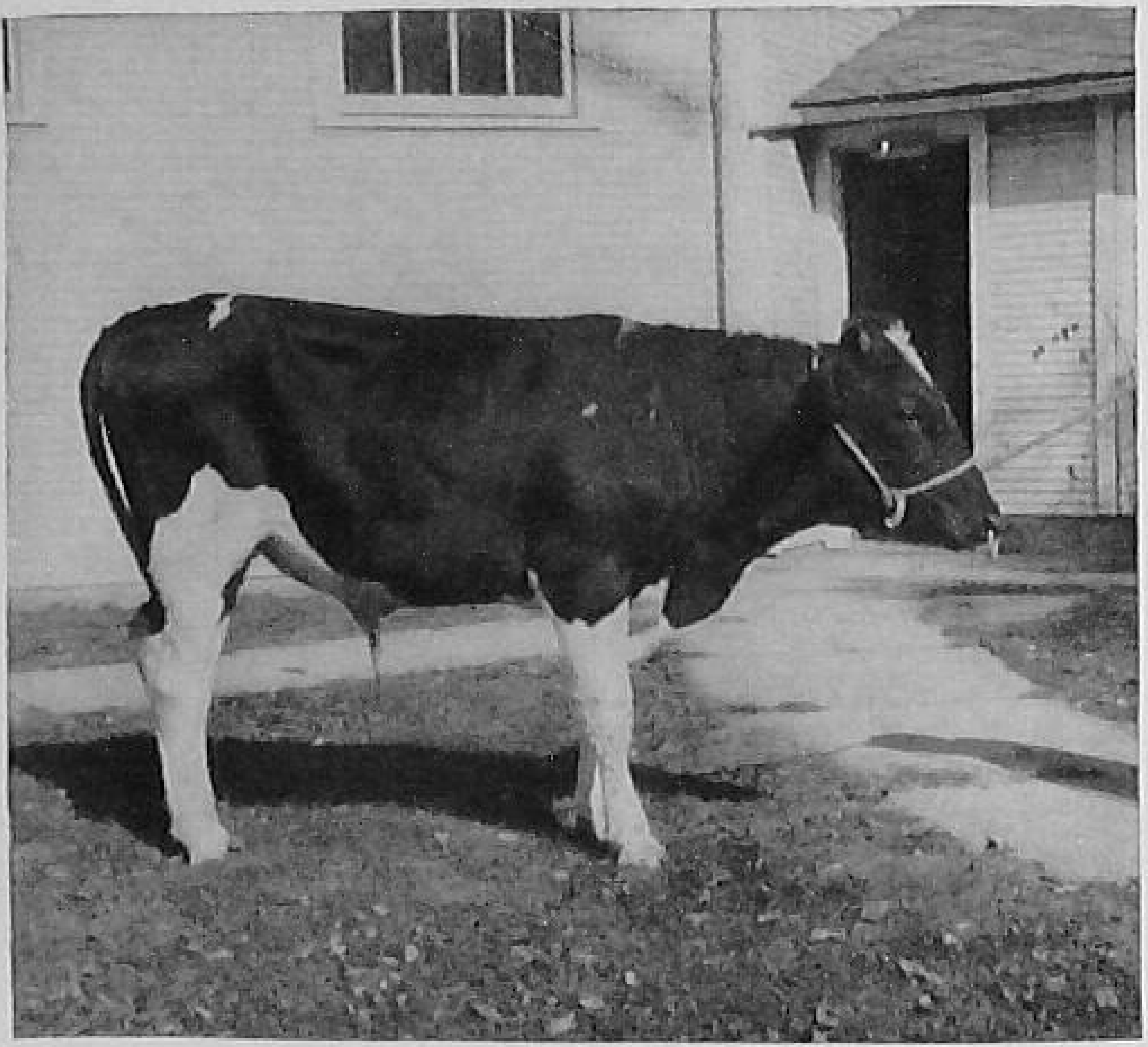


Fig. 68.—Vitamin-A deficient bull. Vitamin deficiencies are not always easily recognized by the untrained observer. This bull exhibited impaired spermatogenesis, night blindness, muscular incoordination and diarrhea, yet his general appearance is not unlike that of many farm bulls.

be repaired following proper therapy (Sutton *et al.*, 1940; Hodgson *et al.*, 1946; Erb *et al.*, 1947).

Although all of the B vitamins are probably not yet known (at least 13 had been named by 1949), it is thought that this important group has little direct effect on reproduction in the larger farm animals, especially the ruminants. In the chicken the B vitamins are likely to be absent or present in suboptimum amounts in some rations, *e.g.*, those containing primarily corn and soybean oil meal. Proper B supplementation of such rations does improve hatchability.

Vitamin C is often present in suboptimal quantities in the diets of man,

monkey, and the guinea pig. The deficiency of this vitamin causes severe debility and even death, yet it is reported that there are no direct effects on fertility in these species. It has been reported that the injection of vitamin C (ascorbic acid) in both bulls and cows which had been classified as "poor breeders" was followed by improved fertility in both sexes. There seems to be current (1949) agreement that the therapeutic benefits of ascorbic acid therapy have not been submitted to a critical test and that judgment must be withheld until more clear-cut evidence is available.

The role of vitamin E in the prevention or treatment of reproductive disorders of the farm animals is still a controversial subject. In the rat and mouse there is no doubt that vitamin E is essential for reproduction. A deficiency of this vitamin prior to puberty results in the absence of spermatogenesis and in testicular atrophy following puberty. In the female conception may occur but abortion follows in the vitamin-E deficient rat or mouse.

FIG. 69.—A severe case of hypothyroidism. Observe the thickening and cracking of the skin.

Numerous reports on the value of wheat-germ oil (a rich source of vitamin E) in the correction of cattle-breeding problems appear in the scientific journals and literally hundreds of testimonials of satisfied users have been published. Attempts to reduce fertility in farm animals by the use of vitamin-E free or deficient rations have not accomplished this purpose. It has been concluded in a report by the National Research Council that, "There is no convincing evidence that the addition of extra vitamin E to normal rations has a direct or specific effect upon reproduction in practical herd and flock management" (Phillips, 1942).

The minerals which are most likely to limit animal growth and health are phosphorous, calcium, and iodine and, in some regions at least, iron, copper, cobalt, and manganese. Of these, phosphorous is most apt to be deficient. Under natural conditions phosphorous deficiency is often complicated by both protein and vitamin-A deficiencies. Under such circumstances reproductive problems are almost certain to occur. In

cattle phosphorous-deficiency symptoms, such as unthriftiness and depraved appetite, usually precede breeding difficulties.

The importance of iodine in the prevention of goiter, the necessity of copper and iron in the prevention of anemia, and the role of calcium in skeletal growth and lactation are such that the diet should always contain them. The relationships of manganese and cobalt to reproduction in farm animals are not known. In areas where the state experiment stations have shown these elements to be deficient, local recommendations should be followed.

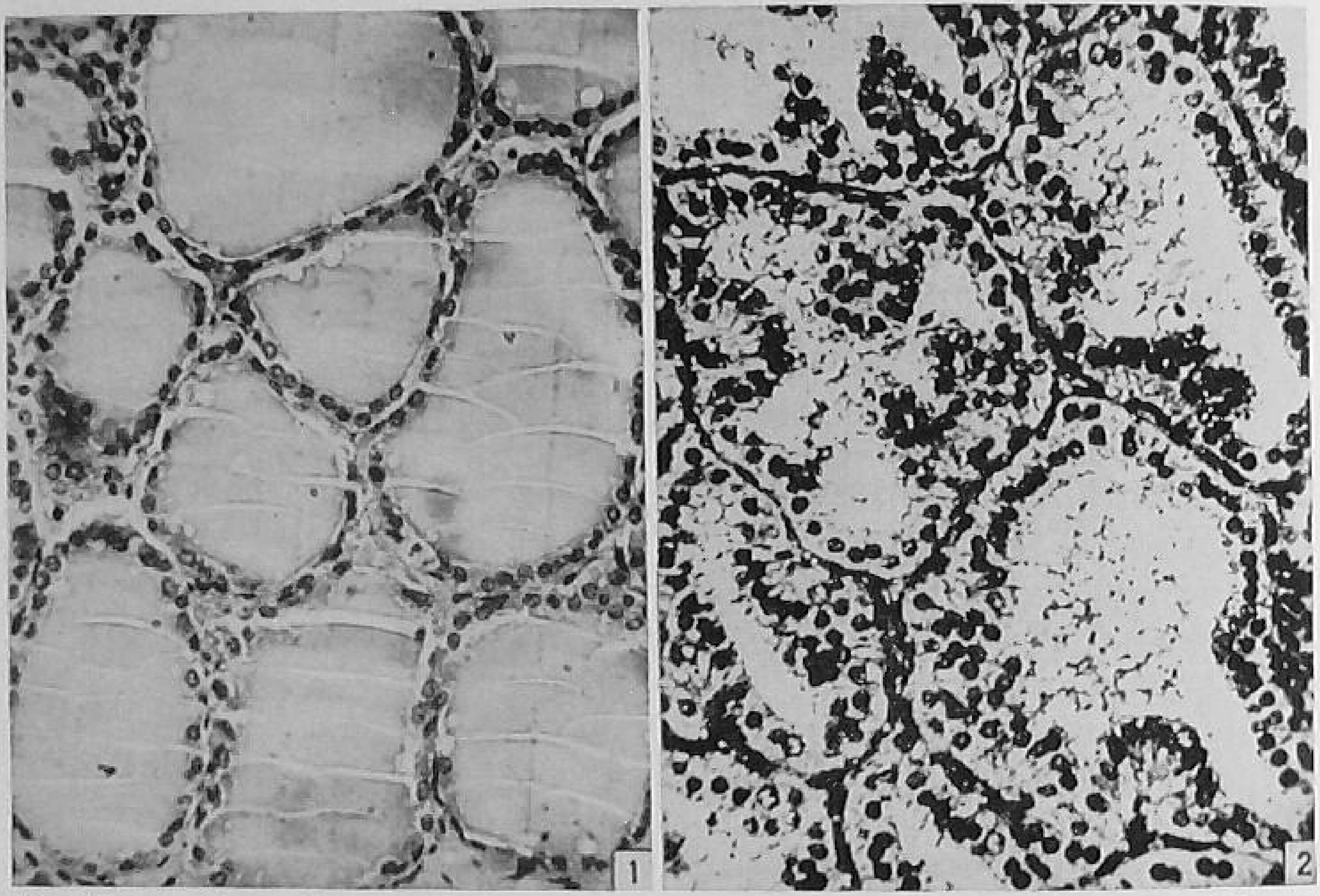


FIG. 70.—1. Normal lamb thyroid. 2. Abnormal lamb thyroid due to iodine deficiency.

Genetic Causes of Sterility.—Certain forms of sterility apparently have a genetic basis. The work of Bridges with Drosophila has shown that a male of sex-chromosome constitution XO (due to nondisjunction) is sterile. Evidently the absence of a Y chromosome in this species renders an animal sterile.

An instance from practical breeding history which appears to belong to this category is that of barrenness in Bates' famous Duchess family of Shorthorns. This family was noted for superior individual excellence, consequently breeders, naturally desirous of maintaining this excellence, followed a practice of breeding within the family, an example of which is given in Fig. 71. But the family was tainted from the beginning with the curse of barrenness. . . . Shortsighted breeders at the time considered it a fortunate circumstance that Duchess cows were so often barren, for it kept down the number of individuals of this favorite

strain and resulted in prices correspondingly high. But as a result of barrenness the strain eventually ran out completely. In Fig. 72 an attempt has been made to show diagrammatically how barrenness was inherited in this family. The diagram is not complete, for it includes only the females in the family. Nevertheless it brings out very forcibly how barrenness occurred very early in the family history, and how it reappeared in about the same proportion of the total population throughout its history. Far from showing an intensification of the defect as a result of inbreeding, this diagram merely illustrates the heredity of a defective family trait.[1]

Probably most breeders of some years' experience can recall certain females in their herds of 10 or 20 years ago that now have no descendants in the herd. If a breeding chart of the herd has been kept or can be made,

Duchess 55th	4th Duke of Northumberland (3649)	Short Tail (2621)	Belvedere (1706)
			Duchess 32nd
		Duchess 34th	Belvedere (1706)
			Duchess 29th
	Duchess 38th	Norfolk (2377)	2nd Hubback (1423)
			Nonpareil
		Duchess 33rd	Belvedere (1706)
			Duchess 19th

FIG. 71.—Pedigree of one of the latest Duchess cows, illustrating system of linebreeding followed in maintaining the family. Duchess 55th produced two calves.

such lines are practically sure of being evident. Some of these lines perhaps disappeared because of poor type or poor production or both. Others, no doubt, have disappeared because of lowered fertility or sterility. Whether this has been due to poor management or to poor genetic make-up is perhaps hard to determine, so to be conservative we will say that some of it has been due to one, some to the other, some to both.

In species characterized by multiple births, fertility and prolificacy are of extreme economic importance. This problem has concerned livestock breeders probably since the domestication of animals and has received the attention of research workers during the last half century. The fact that there are significant differences in the prolificacy of different breeds of swine and between lines within breeds is definite evidence that this trait is heritable. The exact degree of heritability of prolificacy is not known. In some instances where attempts to select for litter size in swine have been made, there has been little increase in prolificacy. Morris and Johnson (1932) found, that in 1,035 litters of Poland-China swine, litter size was increased only one pig per litter during a 20-year period. In a more recent study at the Minnesota Station, Stewart (1945)

[1] BABCOCK, E. B., and CLAUSEN, R. E., "Genetics in Relation to Agriculture," 2d. ed, pp. 555–556. McGraw-Hill Book Company, Inc., New York. 1927.

estimated that the heritability of the number of pigs farrowed is about 17 per cent. In actual practice increasing fertility in an outbred stock of low fertility would be a slow process if simultaneous selection for other characteristics is made. However, even though a heritability of 17 per

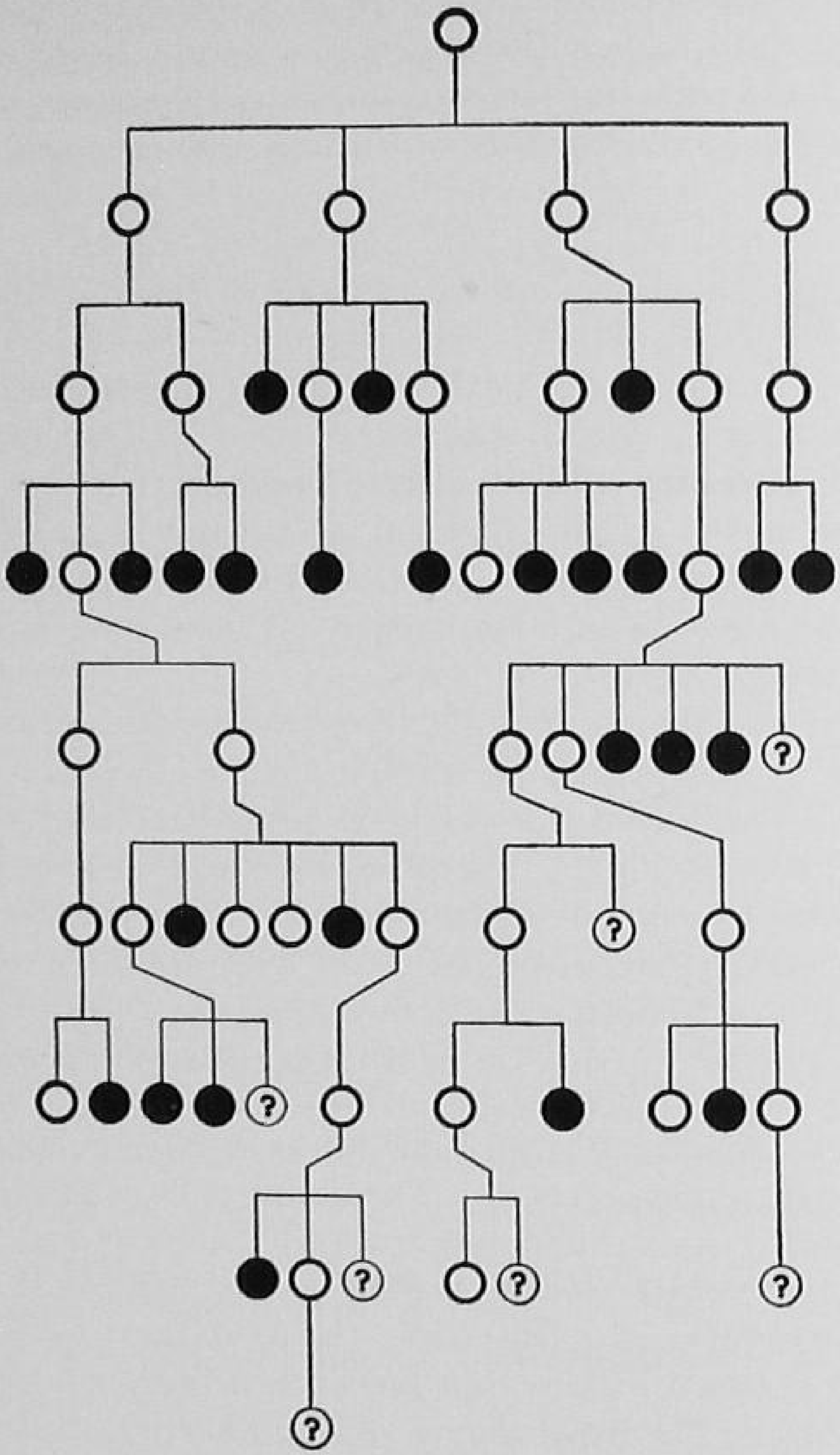


FIG. 72.—Illustrating inheritance of barrenness through the female line of the Duchess family of Shorthorns; barren cows represented by solid black circles. (*From Babcock and Clausen, Genetics in Relation to Agriculture.*)

cent seems low, it does tend to show that breeders have not selected so closely for fertility as is possible. In a companion study of other factors which affect prolificacy of swine, Stewart (1945) found that age and weight of gilts at mating account for 4 per cent of the variance in size of first litters and were of considerable importance in the selection for

fertility. An increase of 10 per cent in the inbreeding of dams of the same age resulted in a decrease of about 0.6 pigs per litter.

The inheritance of functional regulation of reproductive efficiency has been reviewed by Gilmore (1949). This review, containing 142 references, cites data clearly illustrating the fact that the degree of fertility can have a genetic basis. Because of the nature of the data and the complexity of the problem, the *mechanisms* of genetic regulation remain obscure. Of the various factors which may influence fertility or result in sterility, the following have been shown to be heritable: white heifer disease, the freemartin condition, underdevelopment of the gonads, abscence of the gonads or various portions of the genitalia, and intersexuality. A wide variety of lethal factors resulting in fetal or early postnatal death do influence fertility and may be regarded as causes of reproductive failure. Such lethal factors occur in all species.

Systems of Breeding and Sterility.—The fact that too wide crosses, *e.g.*, bison and cattle, or horse and ass, often result in sterile or relatively infertile offspring, coupled with the fact that too close inbreeding often produces similar results as far as sterility is concerned, is further proof that some sterility is caused by genes.

In selecting breeding stock, therefore, one should be careful to make his selections only in strains or families that by their actual records of reproduction have proved themselves to be at least relatively free from genes which lower fertility. It is often observed that animals of a strain which has been closely inbred for a number of generations are sterile when mated among themselves but fertile with other nonrelated strains. In fact, the above condition sometimes applies as well to animals that are not closely related. In a great many of the experiments on inbreeding, there have gradually developed a loss of vigor and a lowering of fertility. For instance, Weismann's and Von Guaita's work with mice gave the following results.

TABLE 14.—DECREASING FERTILITY IN INBRED MICE

Generation	Average Per Litter
1–10	6.1
11–20	5.6
21–29	4.2
29 and 30	3.5
31 and 32	3.6
33 and 34	2.9

Similar work by Ritzema Bos on rats gave the following results:

TABLE 15.—DECREASED FERTILITY DUE TO INBREEDING

1887	1888	1889	1890	1891	1892
$7\frac{1}{2}$	$7\frac{1}{7}$	$7\frac{13}{17}$	$6\frac{21}{36}$	$4\frac{7}{13}$	$3\frac{1}{5}$

This effect of inbreeding is not universal, however, as King reports on two series of rats (A and B) inbred, litter brother and sister, for 25 generations:[1]

> Data given for the A series of inbreds comprise 1,752 litters containing 13,116 individuals, or an average of 7.5 young per litter; records for the B series of inbreds include 1,656 litters, having a total of 12,336 members, or an average of 7.4 young per litter. The two series combined comprise a total of 3,408 litters, which contained 25,452 individuals. For the entire strain the average size of the litter was 7.5 young. . . .
>
> A comparison of the data for the inbred strain with data for litter size obtained from a series of stock Albinos reared under the same environmental conditions as the inbred strain shows that each litter of the stock series was relatively smaller than the corresponding litter in the inbred group. For the entire series of 424 stock litters the average size was 6.7 young per litter. This average is 0.8 less than the average for litter size in the inbred strain.

Crossbreeding, on the other hand, where the resulting individuals are not completely sterile, as is the mule, often produces plants or animals that are more vigorous in all respects than their pure parents and are often more fertile. This increased vigor is termed *heterosis* or *hybrid vigor*. The exact cause of these phenomena in inbreeding and in crossbreeding is not fully understood. It has been suggested, however, that the germ plasm of all species probably carries some inhibiting factors, which, if true, explains why inbreeding often does result in lowered fertility, because these inhibiting factors are intensified, and why crossbreeding often results in increased fertility, because each diverse parent supplies to the offspring factors that tend to dominate and offset the expression of the weak characters supplied by the other parent.

Among species hybrids, there is wide range of ability to reproduce, *viz.*, from a point of increased fertility over the parents down to a point of absolute sterility. The mule and the hinny, the former a jack-mare cross and the latter a stallion-jennet cross, are both sterile, as are also the horse-zebra crosses. Babcock and Clausen report one reference to fertile male hybrids between the zebra and the ass. The researches of Wodsedalek on the reproductive cells of the mule show abnormal reduction divisions during spermatogenesis, which should logically result in imperfectly formed and functioning germ cells. If the hybrids in any cross have characteristically a different number of chromosomes, it is difficult to see how the reduction divisions could be normal and result in the production of functional germ cells. Even if the chromosome numbers were the same in the two species, physiological incompatibility might be present.[2]

[1] King, H. D., "Studies in Inbreeding," Wistar Institute, Philadelphia, 1919.
[2] Babcock and Clausen *Op. cit.*, p. 591.

In many crosses between species of Bovidae, as common cattle with bison, gaur, gayal, and yak, the female is fertile and the male sterile. Among domesticated birds, as in the sterile hybrids between various species of pheasants, the sexual organs are imperfectly formed, and there is a strong suspicion that sterility may be due in part to imperfect sex determination resulting from hybridization. Even aside from this difficulty which is zygotic, there is the further one that the chromosome condition in these hybrids may be unbalanced and the differences in genetic content of the chromosomes may be so great as to prevent functioning of the gametes which are formed. The sterility of species hybrids is in quite a different category from that of the sterility occurring within species.[1]

Davenport observes in regard to hybrids that "it is safe to assume that about all the possible fertile hybrids were long ago produced in nature, and either went down under natural selection or became good species before they came into our hands."

Fig. 73.—Orchitis in a ram. Examination showed that the affected testis had increased in size to the extent that the normal testis had been forced up into the inguinal canal.

Physiological Disturbances.—When the cause or causes of lowered fertility are not readily apparent, they are frequently attributed to physiologic disturbances. Such diagnoses are sometimes made because of a general lack of information regarding the particular condition and sometimes because of the limitations of the diagnostic techniques used. For example, a highly skilled gynecologist might find no *gross* evidences of genital abnormalities as the result of rectal and vaginal examination, and therefore conclude that there were no anatomical or pathological limitations for conception. There might, however, be tissue changes in the Fallopian tubes which would prevent the passage of sperm or ova but which could not be detected except by microscopic post-mortem examination. Likewise, there may be transmissible genital infections which are as yet unrecognized, or vitamin or trace-mineral deficiencies which are still unknown. There are, however, several known physiological disturbances which may prevent normal reproduction.

The failure of the anterior pituitary gland to produce the gonadotropic hormones at the proper time and in the proper amounts will most certainly affect fertility. The absence of ovarian or testicular development and consequent failure of the animal to become sexually mature can

[1] Babcock and Clausen *Op. cit.*, p. 591.

often be explained on the basis of pituitary dysfunction. Likewise, the cessation of the estrual cycle or the loss of sex drive and sperm production in the mature animal may follow pituitary failure. Such animals can sometimes be restored to a breeding condition by the use of the gonadotropic hormones, but the fact that such tendencies may be heritable always raises the question as to the desirability of this approach. Theoretically, at least, abnormal function of nearly any endocrine gland may indirectly affect the reproductive process. Extreme under- or overactivity of the thyroid gland may alter fertility. Abnormal adrenal cortical function may affect general body health and thus secondarily limit reproduction. Tumors of the adrenal gland may produce abnormal quantities of the sex hormones and even bring about sex reversal changes. Tumors or other abnormal growths of the gonads and accessory genital structures may produce abnormal quantities of hormones, especially the steroid sex hormones and gonadotropins, and influence the entire body as well as the genital system.

The above conditions may be difficult to recognize in the farm animals, and accurate data as to their incidence are not available. There are, however, physiologic disturbances which nearly every livestock owner has observed. Among the more common of these is the irregular estrual cycle. The heat periods may occur at very irregular intervals without apparent pattern. In some cases heat does not occur at all, or if it does is of such low intensity that it is difficult to detect. In other instances the heat periods may be abnormally long or short. Even though ovulation may take place and the ova may be viable, the time irregularities make it difficult to have ovulation and copulation coincide. Thus, potentially fertile animals may remain barren. The cause of these irregularities is undoubtedly endocrine and probably involves both the anterior pituitary gland and the ovaries. Seasonal and nutritional factors may be involved.

Abnormal corpus luteum function can affect fertility in at least several distinct ways. As previously described, the corpus luteum may persist in the ovary and continue to secrete progesterone. If progesterone is being produced in large amounts, new Graafian follicles are not formed and estrus and ovulation do not take place. This situation is typical of the lactating sow and the dairy cow during the first part of lactation. In the sow the corpora lutea undergo regression very shortly after weaning the pigs, and in high-producing dairy cows the estrual cycles should be naturally resumed within 40 to 60 days following parturition. The corpus luteum can be removed by ovarian manipulation in cattle, and heat can be induced in sows by the injection of equine gonadotropin. The failure of the corpus luteum to function properly during pregnancy

may prevent implantation of the fertilized ovum or may result in the abortion of the embryo or fetus. Sufficient data are not yet available to justify definite conclusions, but it seems logical to explain some of the reproductive failures which occur in farm animals as due to deficient progesterone secretion.

In cattle, particularly, some females remain in more or less constant heat, will accept the bull, but fail to become pregnant. If this condition persists, the tail head frequently becomes elevated, the animal may bellow a great deal, and behavior may be somewhat more masculine than feminine. The behavior is frequently referred to as nymphomania, meaning unusual sexual desire. The general condition is often called cystic ovary because of the development of large, fluid-filled, thick-walled cysts in the ovaries. These cysts, in contrast to normal Graafian follicles, do not rupture spontaneously, and ovulation does not occur. The condition has been recognized for many years and was formerly treated by the mechanical rupture of the cysts. Following the discovery of the gonadotropic hormones, it was found that the secretion or injection of the follicle-stimulating hormone alone was often followed by the development of very large follicles which did not rupture. The injection of FSH and LH in proper amounts and sequence resulted in both follicular development and ovulation. In light of this knowledge it appears that cystic ovary is probably the result of an endocrine imbalance. Research workers at the University of Wisconsin have found that the injection of special pituitary gonadotropic hormone preparations will cause the rupture of such cysts and will restore a large percentage of nymphomaniac cows to breeding usefulness (Casida *et al.*, 1944).

One of the most perplexing problems in artificial-breeding associations is the "repeat-breeding" cow which shows no detectable genital abnormalities. Some facetiously refer to this problem as "sterility in normal cows." A carefully selected group of 104 such cows was studied at the University of Wisconsin by Tanabe and Casida (1949). These animals were selected by veterinarians experienced in cattle-breeding problems. All animals had been bred at least four times without apparent conception, all had previously calved at least once, were less than ten years old, and were free of genital abnormalities of all types as nearly as could be determined by gross examination, and exhibited estrual cycles of normal length. In order that management might not bias the results, no more than two cows were selected from any one herd. The cows were artificially inseminated and slaughtered on either the third or thirty-fourth day following breeding. At 3 days 66.1 per cent of the cows examined had fertilized ova, but at 34 days only 23.1 per cent had normal embryos. Visible genital abnormalities not detected by clinical exami-

nation were found in 10.6 per cent of the animals and 8 per cent were physical barriers to fertilization. It was concluded that the cows could be divided into three groups, (1) failure of fertilization, 39.7 per cent; (2) embryonic abnormalities and mortality before 34 days, 39.2 per cent; and (3) embryos still normal at 34 days, 21.1 per cent. Exactly why fertilization fails to occur and why early embryonic mortality frequently follows when fertilization does take place have not been satisfactorily answered.

Theoretically, at least, any marked deviation from normal in secretion of estrogen, androgen, or the gonadotropins may affect fertility. When one considers that the entire genital tract of each sex, as well as the gametes themselves, are dependent upon these hormones, this does not seem unusual. Although these hormones have been available for clinical use for at least a decade, thus far their practical applications in both human and animal medicine leave much to be desired in the treatment of sterility. Rapid and encouraging advances have been made, but as previously pointed out, sterility is not a single problem and no one treatment will correct it.

Environment and Reproduction.—Sufficient evidence has already been presented to demonstrate the importance of light and temperature in the regulation of reproduction. The reproductive patterns of the seasonal breeders and the seasonal fluctuations in fertility of the continuous breeders should be thoroughly understood for each species and class of animal if a breeding program is to be carried out most efficiently. The importance of relative humidity and altitude are largely unknown, but it seems safe to conclude that when these factors affect the general well-being of an animal, fertility is likely to be affected.

The hazards of the atomic age to man and animal have received much attention in both the popular and scientific press. Many of the conclusions which have been drawn or hinted at have no basis of fact, but others of equally startling nature have been thoroughly substantiated.

It is indeed interesting to speculate as to the factors which regulate genetic make-up and induce mutations. Whatever these are, they have been going on in a reasonably orderly way for thousands of years. It is well known that proper dosages of X rays and other types of radiation do affect cells, chromosomes, and genes and may alter the rate of mutations. But as to whether whole populations exposed to atomic radiations will become altered or even extinct within a few generations is strictly within the realm of speculation in 1950.

The deleterious effects of X rays upon the testes and ovaries were known as early as 1903. The germinal epithelium is especially sensitive to X rays, and complete and permanent sterility can be produced in

either sex by proper dosage. The degree of damage is proportional to the time and dosage and may vary from temporary lowered fertility to permanent sterility. Exposure of the genital organs to X rays, even for short periods of time, is hazardous and should not be permitted except for excellent reasons and under expert supervision.

During the past 5 years many studies of the effects of externally applied beta and gamma rays and fast neutrons on various body tissues have been made. The data are far from complete and only a few species have been studied. At this writing it appears that the effects of these radiations on the gonads are qualitatively similar to X rays. Numerous experiments of the effects of internally administered radioactive isotopes have been performed. In a general way it appears that the effects of such isotopes on reproduction will depend upon the active life of the isotope, the amount and type of its radiation, the rapidity of elimination from the body, and the types of tissue in which the isotope is concentrated if it is retained in the body (Bloom, 1948).

Summary.—In this chapter we have stressed the difference between sterility and *degree* of fertility and have emphasized the point that sterility and fertility can be influenced by a wide variety of known factors and perhaps an equal or greater number of unknown factors. Anatomical abnormalities of the genitalia can be readily detected and should be regarded as serious and disqualifying defects in breeding stock. Mechanical injuries of the reproductive organs are often the result of careless management and should be guarded against. When injuries do occur, they should be promptly and expertly treated. Transmissible genital diseases, especially brucellosis, are an important cause of economic loss to livestock producers. Since effective diagnostic methods are available for the detection of several of these diseases, the introduction of animals of unknown disease status into healthy herds and flocks, at least without a period of isolation, is risky and inexcusable. The importance of feeding well-balanced rations supplemented with the nutritional factors now known has been discussed. That certain genital abnormalities and level of fertility have a genetic basis is clearly a matter of fact. The frequency and mode of inheritance of some of these conditions are obscure, but the possibilities that the conditions will be transmitted are sufficiently great that rigid selection must be practiced. Some of the more common physiological disturbances and their causes have been discussed.

The breeder's task would seem to be that of selecting his breeding animals from naturally fertile strains; of feeding and managing mature males and females so that viable healthy germ cells may be produced; of growing out his young stock in a sanitary environment and on suitable, complete rations; of attempting to strike an intelligent balance between

production and reproduction; of setting all the barriers possible between his animals and injuries or organisms that might lower their breeding efficiency; of keeping accurate records of all matters pertaining to breeding health and efficiency so that he may know at all times where he stands and in what direction he may be heading.

Finally, it hardly seems necessary to warn against putting our faith in some cure-all of doubtful efficacy and thereby delaying the real job of securing professional service, thus allowing some malady to get a firm foothold. Such a policy is the best possible example of being "penny-wise and pound-foolish."

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CHAPTER VIII

PREGNANCY AND PARTURITION

The factors concerned with the initiation of pregnancy have been discussed in a previous section. The factors concerned with the maintenance of pregnancy and with the birth of the new individual at the time of parturition are of equal importance with conception, since the objective of the livestock breeder is the production of normal, healthy animals capable of efficient milk, meat, wool, egg, or work production. During pregnancy the uterus must undergo considerable modification in size and structure to accommodate the rapidly growing fetus. The uterine muscles must increase in size and numbers but must not be activated too soon lest premature expulsion of the fetus occur. At the time of parturition there must be sufficient relaxation of the birth canal to provide a passageway for the offspring, yet there must be sufficient contractility of the uterine muscles to expel the young quickly and at the same time without damage. In mammals, as described in a separate chapter, the development and function of the mammary glands is an integral part of the reproductive process. The development of the mammary glands is begun at puberty and is completed during pregnancy. The initiation of active milk secretion is ordinarily dependent upon normal parturition, although if the mammary glands are sufficiently developed, copious milk secretion may follow abortion or manipulation of the teats.

Ovarian Hormones during Gestation.—As previously outlined, both estrogen and progesterone are essential for the preparation of the uterine endometrium for implantation of the embryo. Ovariectomy before the uterine lining is prepared will prevent implantation. There are great differences between animals in the dependence of pregnancy on the ovaries. In the mare and woman the ovaries can be removed in early pregnancy without harmful effects, but in the cow, rabbit, and rat the ovaries are essential at least until very late pregnancy. In the pregnant human relatively large amounts of both estrogen and progesterone are excreted in the urine. Urinary estrogens are detectable as early as the first week of pregnancy and reach a peak just before parturition. Most of the urinary estrogen is in the conjugated form as estriol glycuronide and has little physiological activity as such. Progesterone is eliminated in the urine as pregnandiol glycuronide. It is present in small quantities

during the first third of pregnancy and then increases gradually until parturition. Both estrogen and progesterone practically disappear from the urine after parturition.

Endocrine Functions of the Placenta.—There is little doubt that the placenta is an endocrine organ of considerable significance. The hormonal functions of this organ are best understood in woman and the mare. Why these two species should have so much in common and why the other farm animals should differ so much from the mare is as yet unknown. As already discussed, there is little doubt that the placenta can produce estrogens and progesterone. The importance of these hormones in pregnancy is not clear.

Perhaps the most remarkable activity of the human and horse placentae is the secretion of gonadotropic hormones which are very similar to those produced by the anterior pituitary gland. These gonadotropins are secreted by the chorion in the human and the endometrial cups in the mare and are referred to as chorionic gonadotropins or as anterior pituitarylike hormones. In the human the hormone appears in relatively high concentration in the urine during the second week of pregnancy. In the mare the hormone is not present in the urine in easily detectable amounts but is abundant in the blood serum or plasma from the forty-fifth until about the one-hundredth day of pregnancy. This substance is frequently referred to as equine gonadotropin. The physiological response of test animals to the human and horse gonadotropins suggests that the human substance is most apt to cause luteinization and rupture of ovarian follicles and that the pregnant mares' serum produces both follicular growth and ovulation. The purpose of these placental gonadotropins is not clear. In the mare during the period of maximum gonadotropin secretion the ovaries become extremely active and produce numerous Graafian follicles which may rupture and be followed by corpora lutea. Why the mare, a species in which more than one fetus cannot safely develop at any one time, should produce many follicles when pregnant is a biological mystery. Estrus and ovulation are not uncommon in pregnant females of other species but superfetation, the establishment of distinctly separate pregnancies, is a rare phenomenon.

Pregnancy Diagnosis.—The importance of knowing whether pregnancy has been established cannot be emphasized too much. The cessation of the heat periods is nature's first indication that conception has occurred. Pregnant animals fail to come in estrus because of the persistence of the corpus luteum of pregnancy and its inhibition of follicular development. In most instances the failure of estrus to reappear is a reasonably reliable sign of pregnancy. However there are sufficient violations of this rule to make it unreliable for *maximum* livestock-breeding efficiency. In

seasonal breeders the absence of heat may indicate that the ovaries have become quiescent. This is the rule in sheep and occurs in other farm animals, particularly the mare.

If the corpus luteum persists in the nonpregnant female, estrus will not follow. The corpus luteum of lactation, which forms shortly after parturition in cattle and swine, may prevent the reestablishment of the estrual cycle. The implications of this will be discussed later. It is clear, therefore, that more exact methods of detecting pregnancy are desirable.

In species in which manual examination or palpation of the uterus can be made, a trained person can diagnose pregnancy with a high degree of accuracy by the second or third month of gestation. This method is limited to the cow and mare. It is an invaluable aid in the diagnosis and correction of infertility, but unfortunately the supply of qualified diagnosticians cannot meet the need. Other indications of pregnancy, such as the cervical seal, the ascultation of the fetal heart, fetal movements, increased size of the female, or the tendency of pregnant animals to become quiet and to fatten, are either unreliable or require the passage of considerable time before they are useful.

Numerous laboratory tests have been devised for the determination of pregnancy. These are based on the different levels of hormones found in the blood and urine of pregnant females. In the human the Friedman modification of the Ascheim-Zondek test is the one most generally used. It is based on the greatly increased amount of anterior pituitarylike substance found in the urine of pregnant women. The procedure consists of injecting 7 to 10 cc. of morning urine into a mature female rabbit's ear veins at two 12- to 15-hour intervals. The rabbit is then killed at the end of 48 hours and the ovaries removed for examination. The presence of subserous hemorrhagic areas or corpora lutea constitutes a positive reaction, whereas clear retention follicles with no hemorrhagic areas are signs of a negative reaction. This test is positive, in cases of pregnancy, 3 or 4 days after the expected date of the first missed menstrual period. Since estrogen is also produced in increased amounts during pregnancy, its presence in urine, as determined by estrual changes in the vaginal smears from rats, is also used to determine pregnancy.

In the mare, pregnancy may be detected from the fortieth to one-hundredth days of gestation by injecting the mare's serum into immature female rats. A positive reaction is manifest by increased size and activity of the rat ovaries and uterus because of the increased gonadotropic hormone in the blood of pregnant mares. From the one-hundredth day of pregnancy until term, sufficiently large amounts of estrogens are present in mare's urine to cause castrate female rats to exhibit estrus or

spayed mice to show certain vaginal changes when injected with urine of the pregnant mare.

Many modifications of these basic tests have been made. It is possible to diagnose human pregnancy within 5 or 6 hours following the injection of urine into proper test animals. Various chemical tests have been developed for the detection of urinary estrogens in the diagnosis of pregnancy. Unfortunately, no practical laboratory tests for the detection of pregnancy are available for farm animals other than the mare. This is because the hormonal patterns of the other animals differ from the horse.

Other Endocrine Changes.—During pregnancy the pituitary gland, particularly the anterior lobe, increases in weight and activity. Since this gland regulates the activity of the gonads, thyroid, adrenal cortex, and mammary glands, and is of vital importance in growth, protein, carbohydrate, and fat metabolism, it is not surprising that it should be modified during pregnancy.

In the human, and probably other species as well, the thyroid gland becomes markedly enlarged in 50 to 90 per cent of all pregnancies. Increased thyroid activity is necessary in order that the pregnant female may satisfactorily meet the needs of both her own and the tissues of the developing fetus. Insufficient thyroid activity may result in abortion or, in the case of farm animals, hairlessness, weakness, and high mortality during the first few days of life. Thyroid deficiencies are particularly common in the iodine-free areas of the United States, and livestock men in such regions supply pregnant females with iodized salt or potassium iodide to prevent the difficulties described.

The parathyroid glands, which are located on the surface of or adjacent to the thyroid, are directly concerned with calcium metabolism and indirectly with the regulation of phosphorus metabolism. The increased needs of calcium and phosphorus during pregnancy and lactation result in increased parathyroid activity. If calcium is not provided in sufficient amounts, because of dietary inadequacy or underactivity of the parathyroid glands, calcium will be withdrawn from the bones and increased nervousness or severe muscular tetany may result. Milk fever, which is in reality temporary calcium deficiency due to the sudden need of calcium for milk production, is most satisfactorily treated by the intravenous injection of calcium gluconate, which supplies the body needs until the parathyroids become adjusted to regulating calcium metabolism at a new level.

Pseudopregnancy.—Among the most characteristic changes which occur during pregnancy are cessation of the estrus cycle, proliferation of the uterine endometrium, and development of the mammary glands.

These phenomena are observed in several species in the absence of pregnancy. In the rabbit, cat, and ferret, ovulation is normally dependent on copulation. In these species, following mating with a sterile male or mechanical stimulation of the cervix, pseudopregnancy is characteristic. Ovulation, development of the corpora lutea, proliferation of the endometrium, and mammary growth occur. In other words the reproductive and mammary systems assume that pregnancy has been established. In these three species pseudopregnancy lasts for about half the normal gestation period, and estrus cycles are then resumed. In the bitch estrus is followed by a long period of time during which corpora lutea persist. This occurs whether copulation takes place or not. There is extensive mammary development and from external appearances the animal seems to be pregnant. Pseudopregnancy in the dog extends for a period of time equal to normal gestation and is frequently followed by lactation. Milk production does not persist, however, unless suckling is allowed to occur.

Pseudopregnancy of the types described does not occur in the farm animals. Corpora lutea sometimes persist for long periods of time in nonpregnant animals, particularly high-producing cows and lactating swine, but the other characteristics of pseudopregnancy do not occur.

Physiological Regulation of Parturition.—Why parturition occurs at the moment it does remains one of nature's yet unexplained mysteries. Dozens of theories have been developed, but as yet it is impossible to induce parturition at will. It is obvious that the survival of the newborn does not depend upon birth at a *particular* moment. In the human, for example, the *normal* gestation period extends from 220 to 330 days, nor does the gross size of the fetus determine its intrauterine life.

The relative distention of the uterus, pressure of the fetus on the cervix, stimulation of the cervical ganglia, and changes in endocrine balance may all contribute to the termination of pregnancy. In recent years there has been increasing evidence that the hormonal relationships are the determining factor, but even endocrinologists will agree that much is yet to be learned of this process. Estrogen, progesterone, relaxin, and the posterior pituitary oxytocic factor appear to be the chief hormones involved. During early pregnancy estrogen is concerned with the increase in size and numbers of cells in the uterine lining and muscle layers. Since the uterus must be relatively quiescent during pregnancy lest premature emptying take place, it seems logical to conclude that progesterone is necessary for endometrial development and the inhibition of uterine contractions. The fact that pregnancy is usually terminated in the cow following removal of the corpus luteum lends support to this view. The uterine muscle-stimulating factor of the posterior pituitary

gland (oxytocic principle) readily increases uterine contractility under certain conditions, although there seems to be some doubt as to whether it is responsible for the initiation of uterine contractions at parturition. Since it is known that estrogen sensitizes the uterine muscles to the oxytocic factor, it is not surprising that the following theory has developed: The increasing secretion of estrogen during the latter part of pregnancy, followed by a decline in progesterone secretion, culminates in vigorous uterine contractions induced by the posterior pituitary hormone. This theory has much to commend it, but since its application will as yet not induce parturition at will, it can be accepted only with reservations.

Relaxin.—In 1926 Hisaw found that the blood serum of the pregnant rabbit would cause relaxation of the pelvic ligaments of virgin guinea pigs. The principle responsible for this reaction was later found in the blood of pregnant women, mares, and sows, and was extracted from the placenta and corpus luteum. This substance was called *relaxin.* Since relaxation of the pelvic region is characteristic of parturition, the possibility that this hormone has a vital role in the birth process should not be overlooked. Because of the wide variation in the source of relaxin, there was considerable controversy about its existence and function. Recent work of Hisaw *et al.* (1944–1946) indicates that relaxin is a separate hormone and is not a steroid as are the estrogens and progesterone. The uterus appears to be concerned in the production of relaxin and seems to be dependent upon progesterone in carrying out this function.

Significance of Parturition to the Livestock Breeder.—The period of parturition is one of the most critical stages in the life of any animal. All the advantages gained in selecting genetically desirable and healthy parent stock and providing the very best of environmental and nutritional conditions throughout pregnancy can be dissipated at parturition through carelessness or ignorance. Death takes a large toll during parturition. Some animals are too weak to survive the birth process, others die because of mechanical injury or suffocation, and others are lost due to the rigors of the environment. In still other instances the young and dam alike may subsequently suffer from damage and infection incurred during or following parturition. It is not the intent of the writers to train veterinary obstetricians but to describe the normal process of birth and the recognition of complicated or difficult parturition.

Place of Parturition.—Because of the ever-increasing complexity of the delivery room in the modern hospital, we tend to consider the development of more and more elaborate maternity stalls as desirable. There is little experimental evidence to justify this view in practical livestock production. If environmental conditions are favorable and there are no known complications of delivery anticipated, by far the best place for

mares and cows to drop their young is in a clean, nutritious pasture. In order that there may be no doubt as to meaning, a crowded exercise lot adjacent to the barn is not considered a clean pasture nor is a heavily wooded lot with growthy underbrush considered desirable. In the Western range states cattle and horses are expected to remain away from the barns while giving birth, and it has long been recognized that the infection of the young is most apt to occur when parturition takes place in or around ranch buildings. The obvious disadvantages of this practice are uncertainty of weather conditions and the fact that difficult birth may not be known until it is too late to render assistance.

During parturition ewes should be kept under fairly close surveillance in a lambing pen, and sows should be shut up by themselves in a house or pen. With proper thought and care the advantages gained, in all classes of livestock, from giving birth in the open can be duplicated in the maternity stall or pen with the distinct added advantage that assistance can be given if it is required. Maternity stalls or pens should be planned so as to give the highest degree of safety to the dam and her offspring and the greatest degree of convenience to the caretaker. The stall or pen should be roomy, and there should be no protruding constructions that might lead to injuries. Mares sometimes lie down at parturition with their buttocks against a wall and some breeders obviate this possibility by building false walls that can be quickly moved. Doors into maternity stalls should be as wide as possible, in order to prevent injury to pregnant females. Maternity barns or pens should be well ventilated, easily cleanable, and located where the animals contained can see and hear other animals with which they have been kept. Under no circumstances should parturition take place in a stanchion.

The heavy death losses which occur in swine at or following parturition have focused the attention of swine producers and research workers on this problem. Surveys of these losses on corn-belt farms have shown that at least 20 to 30 per cent of all pigs which are farrowed are dead or die within the first few days of life. Some of these losses are due to nutritional deficiencies during gestation, others may have genetic, physiologic, or pathologic causes, and still others may be due to injury or chilling of the pigs. As a result of these losses more innovations have been introduced to assist parturition in the sow than in all other farm animals combined. Most farrowing pens have guard rails about 8 in. from the wall and 8 in. from the floor to prevent the sow from crushing her pigs against the wall. Concrete floors, unless well insulated or heated, are usually best covered with planks or a plank platform provided for the sow. One of the most effective methods of reducing losses due to chilling and crushing is to provide heated brooders or hovers in one

corner of the pen. This not only prevents chilling but provides a safe place for the pigs to lie when they are not suckling. The heat lamps, which are produced by several electrical manufacturers, provide a cheap but satisfactory source of heat for such brooders. The observation that sows usually lie with their backs uphill has led to the use of pens with sloping floors. Swine producers report reduced losses when such arrangements are provided. One of the newest developments is the use of the farrowing crate. Based on the theory that a sow which cannot move about freely or turn around would be unlikely to injure the newborn pigs, several types of crates which restrain the activity of the sow have been produced. Numerous swine producers in the Midwest used such contrivances during 1949, and only time will prove their merit. That man is ingenious is apparent; whether he will be able to improve on nature's best conditions remains to be seen.

Sanitation.—All maternity stalls or pens should be built or arranged so that maximum advantage can be taken of the most efficient germicide and also the most efficient growth promoter known, *viz.*, sunshine. Before putting any female into a maternity stall or pen, both the animal and the pen should be thoroughly washed with a disinfectant solution. The coal-tar disinfectants, such as cresol, are good for this purpose, a 2 per cent solution to be used on the animal and a 5 per cent solution on the stall. The young are quite likely to suck or lick various parts of the mother's body; therefore, her whole body, more particularly the teats, should be kept clean. The floor and walls should be scrubbed thoroughly, care being taken to work the disinfectant well into the cracks and corners. Fresh, clean bedding should be used, preferably straw or hay rather than sawdust or shavings, as either of the latter is quite likely to get into the stomach or lungs of the newborn and cause inflammation. For sows, the hay or straw must be short enough so that the pigs cannot burrow under it, thus becoming hidden from view and running the risk of being trampled to death.

If brucellosis, contagious abortion, is known to exist in the cattle or swine herd, special care must be given all maternity stalls. The genital discharges and fetal membranes of infected animals are one of the most potent sources of spread of the disease to other animals and to the human. Any aborted material should be regarded with suspicion and the cause of the abortion should be investigated by a veterinarian.

Time of Parturition.—A very necessary condition for successful parturition is that the breeder know when to expect it, and this predicates the keeping of a record of the breeding of all females. The record book, coupled with a knowledge of the normal gestation period and a sharp lookout for the unexpected, will enable the breeder to have things in

TABLE 16.—GESTATION TABLE

Date bred	Mare, 336 days	Cow, 281 days	Sow, 114 days	Ewe, 147 days
Jan. 1	Dec. 3	Oct. 9	Apr. 25	May 28
Jan. 6	Dec. 8	Oct. 14	Apr. 30	June 2
Jan. 11	Dec. 13	Oct. 19	May 5	June 7
Jan. 16	Dec. 18	Oct. 24	May 10	June 12
Jan. 21	Dec. 23	Oct. 29	May 15	June 17
Jan. 26	Dec. 28	Nov. 3	May 20	June 22
Jan. 31	Jan. 2	Nov. 8	May 25	June 27
Feb. 5	Jan. 7	Nov. 13	May 30	July 2
Feb. 10	Jan. 12	Nov. 18	June 4	July 7
Feb. 15	Jan. 17	Nov. 23	June 9	July 12
Feb. 20	Jan. 22	Nov. 28	June 14	July 17
Feb. 25	Jan. 27	Dec. 3	June 19	July 23
Mar. 2	Feb. 1	Dec. 8	June 24	July 27
Mar. 7	Feb. 6	Dec. 13	June 29	Aug. 1
Mar. 12	Feb. 11	Dec. 18	July 4	Aug. 6
Mar. 17	Feb. 16	Dec. 23	July 9	Aug. 11
Mar. 22	Feb. 21	Dec. 28	July 14	Aug. 16
Mar. 27	Feb. 26	Jan. 2	July 19	Aug. 21
Apr. 1	Mar. 3	Jan. 7	July 24	Aug. 26
Apr. 6	Mar. 8	Jan. 12	July 29	Aug. 31
Apr. 11	Mar. 13	Jan. 17	Aug. 3	Sept. 5
Apr. 16	Mar. 18	Jan. 22	Aug. 8	Sept. 10
Apr. 21	Mar. 23	Jan. 27	Aug. 13	Sept. 15
Apr. 26	Mar. 28	Feb. 1	Aug. 17	Sept. 20
May 1	Apr. 2	Feb. 6	Aug. 23	Sept. 25
May 6	Apr. 7	Feb. 11	Aug. 28	Sept. 30
May 11	Apr. 12	Feb. 16	Sept. 2	Oct. 5
May 16	Apr. 17	Feb. 21	Sept. 7	Oct. 10
May 21	Apr. 22	Feb. 26	Sept. 12	Oct. 15
May 26	Apr. 27	Mar. 3	Sept. 17	Oct. 20
May 31	May 2	Mar. 8	Sept. 22	Oct. 25
June 5	May 7	Mar. 13	Sept. 27	Oct. 30
June 10	May 12	Mar. 18	Oct. 2	Nov. 4
June 15	May 17	Mar. 23	Oct. 7	Nov. 9
June 20	May 22	Mar. 28	Oct. 12	Nov. 14
June 25	May 27	Apr. 2	Oct. 17	Nov. 19
June 30	June 1	Apr. 7	Oct. 22	Nov. 24
July 5	June 6	Apr. 12	Oct. 27	Nov. 29
July 10	June 11	Apr. 17	Nov. 1	Dec. 4
July 15	June 16	Apr. 22	Nov. 6	Dec. 9
July 20	June 21	Apr. 27	Nov. 11	Dec. 14
July 25	June 26	May 2	Nov. 16	Dec. 19
July 30	July 1	May 7	Nov. 21	Dec. 24
Aug. 4	July 6	May 12	Nov. 26	Dec. 29
Aug. 9	July 11	May 17	Nov. 31	Jan. 3
Aug. 14	July 16	May 22	Dec. 6	Jan. 8
Aug. 19	July 21	May 27	Dec. 11	Jan. 13
Aug. 24	July 26	June 1	Dec. 16	Jan. 18
Aug. 29	July 31	June 6	Dec. 21	Jan. 23
Sept. 3	Aug. 5	June 11	Dec. 26	Jan. 28
Sept. 8	Aug. 10	June 16	Dec. 31	Feb. 2
Sept. 13	Aug. 15	June 21	Jan. 5	Feb. 7
Sept. 18	Aug. 20	June 26	Jan. 10	Feb. 12
Sept. 23	Aug. 25	July 1	Jan. 15	Feb. 17
Sept. 28	Aug. 30	July 6	Jan. 20	Feb. 22
Oct. 3	Sept. 4	July 11	Jan. 25	Feb. 27
Oct. 8	Sept. 9	July 16	Jan. 30	Mar. 4
Oct. 13	Sept. 14	July 21	Feb. 4	Mar. 9
Oct. 18	Sept. 19	July 26	Feb. 9	Mar. 14
Oct. 23	Sept. 24	July 31	Feb. 14	Mar. 19
Oct. 28	Sept. 29	Aug. 5	Feb. 19	Mar. 24
Nov. 2	Oct. 4	Aug. 10	Feb. 24	Mar. 29
Nov. 7	Oct. 9	Aug. 15	Mar. 1	Apr. 3
Nov. 12	Oct. 14	Aug. 20	Mar. 6	Apr. 8
Nov. 17	Oct. 19	Aug. 25	Mar. 11	Apr. 13
Nov. 22	Oct. 24	Aug. 30	Mar. 16	Apr. 18
Nov. 27	Oct. 29	Sept. 4	Mar. 21	Apr. 23
Dec. 2	Nov. 3	Sept. 9	Mar. 26	Apr. 28
Dec. 7	Nov. 8	Sept. 14	Mar. 31	May 3
Dec. 12	Nov. 13	Sept. 19	Apr. 5	May 8
Dec. 17	Nov. 18	Sept. 24	Apr. 10	May 13
Dec. 22	Nov. 23	Sept. 29	Apr. 15	May 18
Dec. 27	Nov. 28	Oct. 4	Apr. 20	May 23

readiness for the reception of the newborn. In some instances a knowledge of breeding date and of gestation period is not enough to ensure that everything shall be in readiness, but without this information the case is well-nigh hopeless.

If a stall or pen is to be used, the females should be watched with even more diligent care than usual as the time for parturition approaches. They should not at this time be subjected to sudden changes of any kind in feed, exercise, or care. Moderate exercise is necessary to keep the muscles in good tone and to prepare them for the strain that lies ahead. The feed should be of a somewhat laxative nature—this point cannot be overstressed. The droppings must be watched closely, and if, even in spite of proper selection of feeds, constipation develops, it must, for the safety and well-being of both mother and offspring, be quickly remedied. Feeds indicated at this time are pasturage, silage, roots, legume hays, bran, linseed-oil meal, and ground oats. In case of emergency, linseed oil or epsom salts may be administered. An abundance of good drinking water is also essential.

TABLE 17.—ESTRUS—GESTATION RELATIONS

	Estrual cycle in days	Gestation, days	Ratio estrual cycle to gestation
Mare	21	336	1:16
Cow	20	280	1:14
Ewe	16–17	148–153	1: 9
Sow	19	112–114	1: 6

When bred, animals should be in fairly thin condition, but they should be gaining and should continue to gain slowly all through the gestation period, coming to the time of parturition in good condition regarding both quality and amount of flesh. Extremes in thinness as well as fatness should be sedulously avoided.

The female should be separated from the herd at least 1 to 3 weeks before parturition, so that danger of violent contact may be avoided. This will also enable the breeder to watch more closely and will provide opportunity for the animal to become accustomed to the stall or pen where parturition is to occur. Animals are naturally more or less nervous at this time, and it is necessary that everything possible be done to allay their fears, which conduces to ease of parturition as well as to the safety of the newborn.

Preliminaries to Parturition.—Animals generally evidence a loosening of the ligaments and muscles in the pelvic region just previous to parturi-

tion, this being more noticeable in mares and cows. The pelvic region relaxes, the tail rises, the flanks and croup become hollow, and the enlarged abdomen drops. At this time, animals spring in their middles and start to make bag, with the udder becoming hard and tender, especially in primiparae. If the congestion in the udder becomes too great, it should be relieved by milking before parturition. Most animals give evidence of approaching parturition by their general nervousness and fickle appetites. The mare whisks her tail, the cow bellows, the ewe bleats, and the sow grunts plaintively. Movements of the fetuses are often observable through the body wall or recognizable to touch. If not restrained, the female at this time will seek seclusion from its fellows, and the sow often starts to pick up straw, sticks, etc., with which to build a nest. Individuals, of course, vary in these manifestations, sometimes beginning to react a considerable time before parturition is due. However, these patterns of behavior and the breeder's record book of dates of matings taken together do give ample and accurate warning.

Act of Parturition.—If everything is normal and the animal has been properly fed and cared for, the act of parturition can usually be accomplished without assistance. Under these conditions the best procedure for the manager or herdsman, after checking up and seeing that all details have been properly carried out, is to go on with his work and let nature take its course. Here again the happy medium between too much attention and too little should be the aim. Meddling is often dangerous alike to parent, offspring, and owner. On the other hand, the day of parturition is rather a poor one to choose for a holiday. Mere human presence at this time is often objected to by the animal, especially by mares, which are particularly sensitive to human presence and will delay foaling as long as possible if such persists. Other animals, though not so sensitive, also prefer seclusion at this time. An occasional visit to note progress of events is always desirable and often profitable, and at this time an invaluable asset is the animal's confidence in her caretaker.

Parturition may be divided into several phases. The first phase consists of the dilation of the cervix and the loosening of the pelvic region. The second phase consists of the gradually accelerating contractions of the uterine and abdominal muscles causing the actual expulsion of the fetus. The third stage is a continuation of the second, the muscular contractions beginning to abate but resulting in the expulsion of the afterbirth. A convalescent phase covers several days during which the uterus, cervix, and pelvis gradually return to the normal nonpregnant state.

Labor pains set in from 1 to a few hours before final expulsion of the fetus. They are mild at first, lasting from a few seconds to 1 or 2 minutes with intervals of 15 minutes between. Their tempo, duration, and

strength are gradually accelerated. The animal becomes increasingly restless and nervous, shows evident signs of pain, and the skin becomes hot and dry. The pains are caused by rhythmic contractions of the longitudinal muscles in the wall of the uterus, which in this way begin the dilation of the cervix to allow passage of the fetus. The dilation of the os is soon followed by the contraction of all the uterine muscles, as well as the abdominal muscles and the diaphragm, the contractions being followed by a short period of calm for rest. The combined contractions of the uterine and abdominal muscles soon force out the fetal membranes, which act as an elastic wedge to open the passages gradually. After protrusion, the water bag soon breaks, releasing part of the fluid; and the

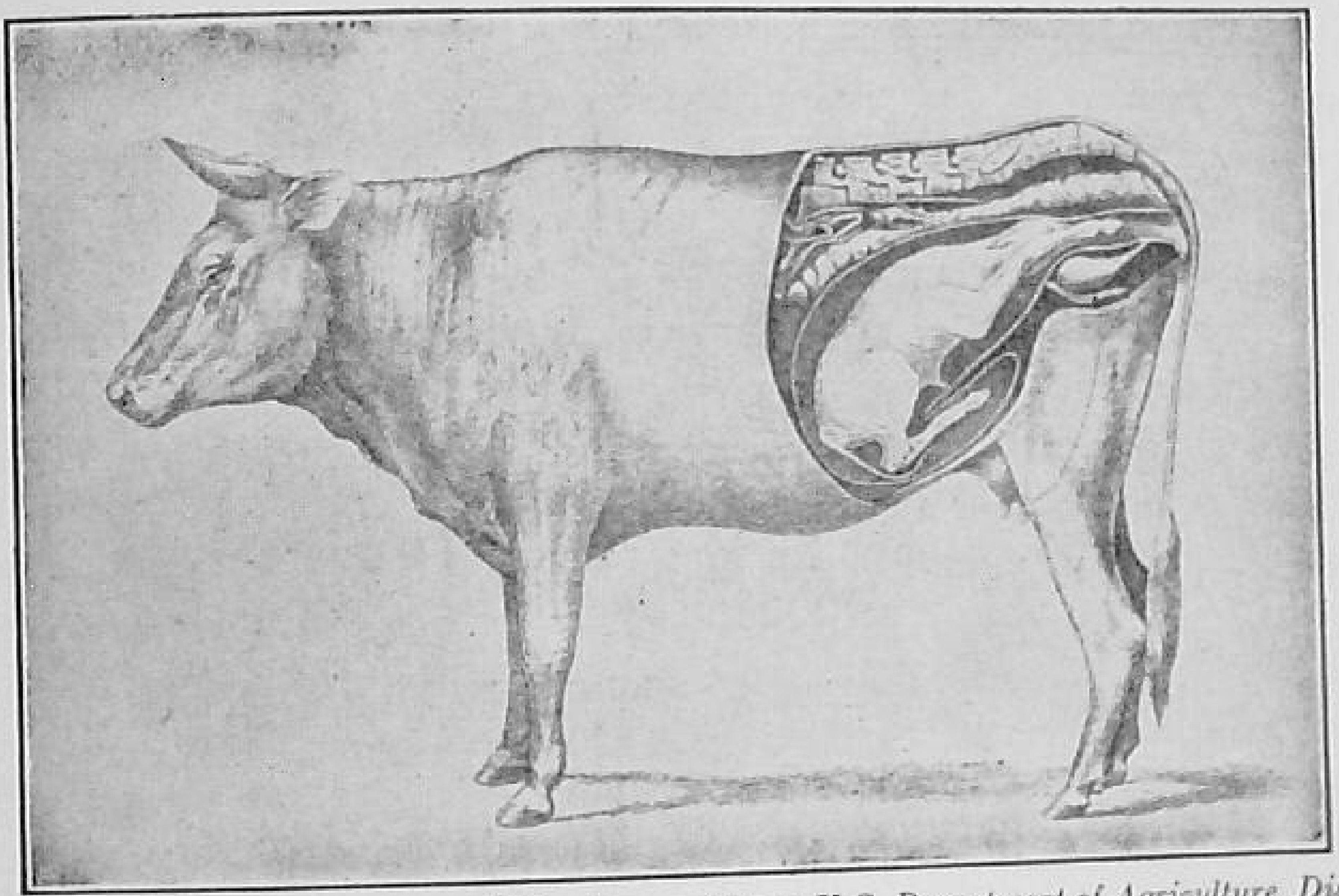

FIG. 74.—Normal position of calf in utero. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

young, which in the meantime has turned first onto its side and then all the way over onto its stomach, soon makes its appearance.

The duration of parturition varies in different species of animals, being in the mare normally from 5 to 30 minutes; in the cow, 1 to 2 hours; in the ewe, 15 to 30 minutes for each lamb born; and in the sow, 10 to 30 minutes for each pig, with sometimes an interval up to an hour between the pigs.

The last stage of parturition consists of the expulsion of the fetal membranes, or afterbirth, and the man in charge should keep a careful watch to see whether or not this occurs normally. This may follow soon after birth, but, if it is delayed more than 24 hours, or 48 at the outside, steps should be taken to ascertain and obviate the difficulty. When expelled, the afterbirth should be removed at once and buried or burned. If this

is not done, many sows, cows, and even some mares will eat this material. If, as sometimes happens, the young are born in the intact membranes, they should be liberated immediately in order to prevent asphyxiation.

The mare, cow, and ewe give birth either standing or lying, the sow reclining.

Types of Presentation.—The two normal presentations of a fetus are front feet first with the head resting between or on the knees, or hind feet first, the first-named being the most usual and showing the least complications. The pelvic passage is generally large enough to permit fairly easy passage of the forefeet and head. It is none too large, however, for the largest portion of the fetus, *viz.*, the thorax and shoulders. After the head has passed the vulva, there is often a short pause before the much greater effort now required. The dorsal vertebral spines over the shoulders are compressed backward, the thoracic cavity contracted and elongated, which diminishes its vertical diameter and permits passage through the pelvis. The posterior portion of the fetus generally passes through the pelvis without difficulty.

The normal hind-feet presentation, with the fetus lying on its belly and its back uppermost, is not quite so favorable as the anterior presentation. Birth usually takes longer with this presentation, and the pinching of the umbilical cord may result in asphyxiation.

There may be various types of malpresentations, such as a buttocks presentation, back presentation, all four feet presented, and many others, some of which are shown in Fig. 75. Any malpresentation requires early recognition, together with a lot of skill and patience on the part of an experienced person, in order to prevent the death of the fetus and/or its dam.

Assistance at Parturition.—If, after reasonable time and effort have been expended, a female appears to be making no progress in parturition, it is advisable that an examination be made so that proper assistance may be rendered before the animal has completely exhausted her strength in futile efforts at expulsion. For such an examination the external parts of the vulva should be well cleaned, the hand and arm should be thoroughly cleansed and lubricated, and the fingernails cut short. After proper precaution has been taken against injury, the hand, fingers held in a cone shape, is inserted into the vagina. There may be various types of malpresentations, such as only one front leg with the other turned back, one hind leg and the other stretched forward, abdominal or sacral presentation, head turned back on the side, head protruding with forelegs retained, all four feet presented, etc.

The cardinal features in the work of correcting the position of a fetus are cleanliness, quietness, gentleness, and perseverence, backed up, of

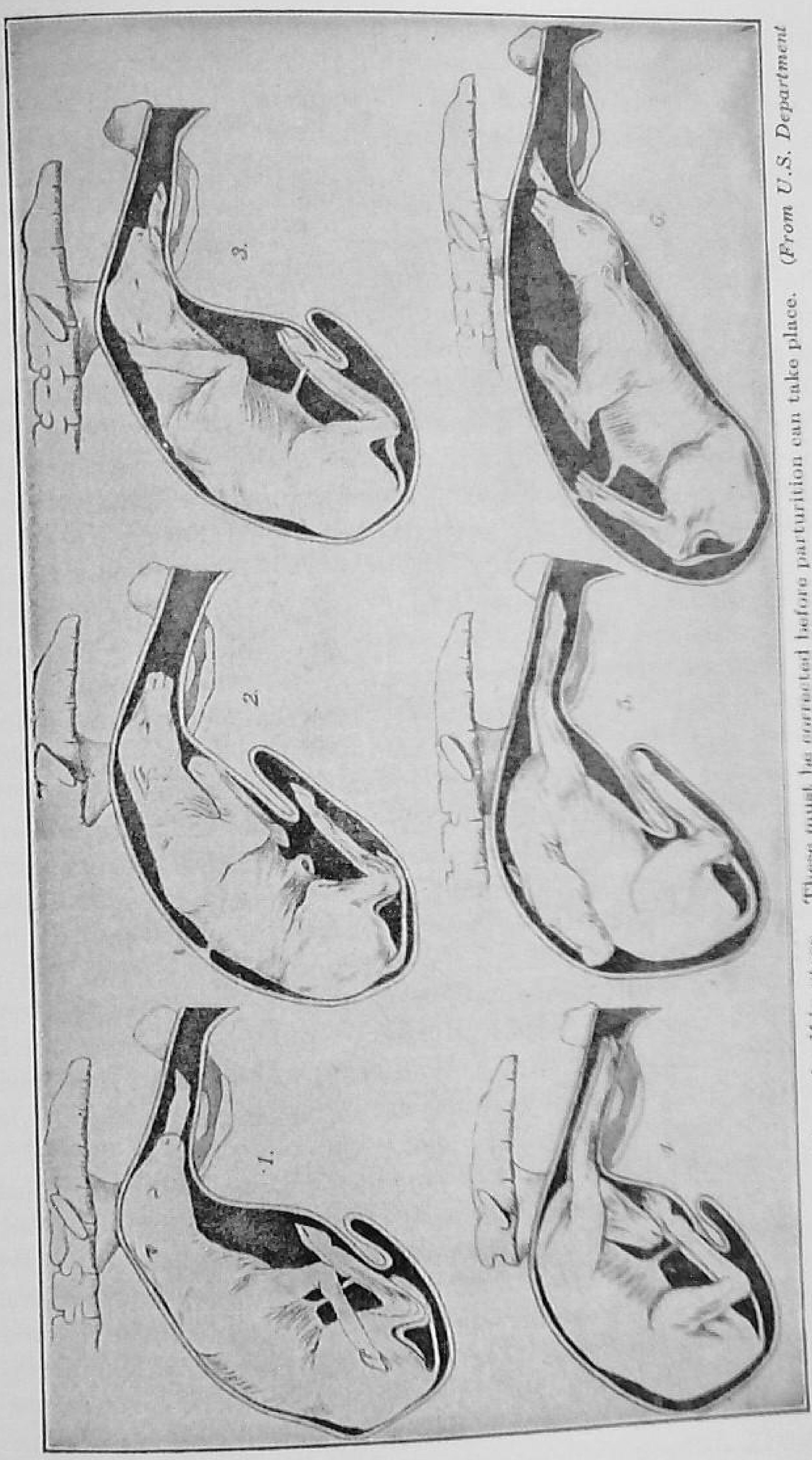

FIG. 75.—Abnormal positions of calf in utero. These must be corrected before parturition can take place. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

course, by *knowledge, skill,* and *experience.* If the presentation is normal, strength for expulsion merely being lacking, the feet can be grasped and a pull exerted downward and backward in conformity with the shape of the pelvis and the position of the young. The pull should only be exerted at the time the dam is in labor, never in the rest periods, except to maintain the gain that has been made. In correcting an abnormal presentation, it is often necessary to push the young well forward into the uterus, and this should be done gently and during the rest period, not during the labor period. A small clean rope can be used to slip around the feet of a colt or calf, and a piece of No. 9 wire with one end bent into a hook to catch under the lower jaw is often useful as a last resort with lambs or pigs.

When parturition is unduly delayed or retarded, the fetus often dies. This may be due to twists or knots in the umbilical cord or to too long a stay in the passage, leading either to the stoppage of fetal circulation, or the depriving of the fetus of a supply of oxygen, or both. The same result is likely to follow premature breaking of the water bag with the consequent uterine pressure on the fetus or the too early disunion of the fetal membranes and the uterus of the mother. When labor has once started, it should be expedited in every manner that is not inimical to the safety of the fetus. The experienced caretaker can often cheat death through his own efforts, but there is no other time at which a skilled veterinarian can be of greater value to the progressive breeder.

Care of the Young at Parturition.—If birth is normal and the young are normal and vigorous, interference is not advisable. A colt or calf should be on its feet and sucking within an hour after birth, but, if not, some assistance may be given so that the young animal can begin to get nourishment. The same applies also to lambs, where, in case of twins, the shepherd generally removes the first lamb until parturition is complete, when both lambs are allowed to nurse. In the case of sows, it is advisable for the herdsman to be present at parturition in order to remove the pigs when born, dry them, and put them in a warm safe place until parturition is complete, when all are allowed to nurse.

Losses from various forms of sterility are severe enough without adding to them by negligence at the time of parturition. Sometimes it is necessary to remove the young from the membranes so that they can start breathing; whereas, on other occasions, it is necessary for the same reason to remove mucus from the mouth and nostrils. Many animals apparently stillborn can be induced to start breathing by slapping the sides, working the front legs and chest, as in restoring a man who has been submerged in water, blowing into the nostrils, tickling nostrils with a feather, etc. If an animal is stillborn, vigorous action on the part of the attendant will

often cheat death, as will protection from the elements for those which have safely arrived.

Cleanliness of the stall, the dam, the owners' hands, and any instruments which might be used are essential. As previously mentioned, the mother should be thoroughly cleaned before parturition. The mammary glands should be clean. Many livestock men dip the umbilical cord in iodine soon after birth to assist in preventing navel infection, or scours, but the most effective means, as stressed, are cleanliness of the surroundings.

Many swine producers clip or remove the sharp "wolf" teeth of newborn pigs. Although these teeth appear to serve no useful purpose, their removal sometimes results in injury or infection of the jaws and they should not be removed unless they injure the teats of the sow.

Care of the Mother at Parturition.—The general care and feeding of the parturient animal will of necessity vary with the species and with the local conditions. It is obvious that the requirements of a cow calving on pasture in June are quite different than a sow farrowing in January. Without attempting a treatise on management and nutrition, a few basic principles will be summarized. After safely delivering her young, the things a female needs most are rest and quiet, together with a moderate amount of temperate water. She should not be fed for 12 to 24 hours after parturition and should be started on feed very gradually. Gruels of bran and ground oats with perhaps a little linseed-oil meal are good at this time, together with a small amount of good-quality leguminous hay and some pasturage. The feed must be moderate in amount for two reasons: (1) A return to the normal condition of the dam's system will be hindered by overfeeding, and (2) the presence of too much milk in the udder as a result of overfeeding is sure to cause scouring in the young, which is always a serious drawback to normal health and growth. The wise herdsman never feeds a nursing female until he has observed the character of the droppings of the young, and at the first sign of scouring, the dam's feed should be reduced.

One of the most common disturbances of high-producing cattle is milk fever. This condition is actually not accompanied by fever but is recognized at first by general depression of the cow, followed by nervous excitation. Twitching of the muscles occurs and is followed by collapse and eventual loss of consciousness. These symptoms are caused by a subnormal amount of calcium in the blood which is believed due to the sudden drain of milk secretion on the stores of body calcium. It can be successfully treated by the intravenous administration of calcium gluconate. For this reason it is unwise to completely milk cows following

calving. It is necessary, however, to see that some milk is drawn from all quarters in order that excessive pressure does not injure the udder. There is still controversy as to whether cows should be milked prior to calving. If there is evidence of extreme mammary congestion, the relief of the pressure by partial milking should be considered. In general, prepartum milking is to be discouraged because of the great value of colostrum to the calf.

In general about 2 weeks should be allowed to get the dam back on full feed. Mares can go back to light work in 2 weeks. Care must be exercised that the foal left in the stall cannot harm itself, because it will be restless without its dam. When mares are at work, the foal should be allowed to nurse at midmorning and midafternoon after the mare has been cooled off, if warm, and after her udder has been washed.

If genital discharges persist following parturition, particularly if these are bloody or foul smelling, the possibility of infection should not be overlooked. With valuable breeding animals, routine genital examinations by a veterinarian specialized in reproductive problems can be considered a wise investment. As the proverbs "stitch in time" and "ounce of prevention" have proved true, so too can the prevention or early correction of genital disorders be expected to increase breeding efficiency.

Feeding and Care of the Newborn.—As knowledge of the nutritional requirements of man and animals is gained, it becomes increasingly difficult to know when the effects of nutrition first make themselves felt on embryonic and fetal development. It seems likely that the pregestational care and feeding of the female can affect the young. It is now established that the anterior pituitary gland of the newborn calf can be permanently affected by vitamin-A deficiency of the pregnant dam. The damage cannot be repaired by subsequent administration of vitamin A. The possibility exists, therefore, that malfunctions which might manifest themselves in a pregnant or lactating animal might have been caused during the fetal development of the animal itself.

The importance of the proper nutrition of all animals which are to be used for breeding purposes cannot be overstressed. Not all the nutritional requirements are yet known, but it goes without saying that the animals should be fed according to the recognized standards of the day.

Assuming that the young are normal and vigorous at birth, the breeder can do much to keep them that way. For a time following parturition newborn mammals are dependent almost entirely upon milk. The first milk produced following parturition is quite different than ordinary milk. In cattle colostrum is about five times as high in protein and twice as high in fat and minerals as ordinary milk. It is especially high in globulin and contains antibodies which tend to protect the young from various micro-

organisms. Cattle colostrum contains ten times as much vitamin A and three times as much vitamin D as ordinary milk and over ten times as much iron. Although some species, such as the guinea pig, are apparently benefited little by colostrum, it is regarded as highly desirable that the farm animals receive it. If for any reason colostrum is not available, as in the case of animals milked prepartum or in the case of death of the dam, the young should be fed colostrum from another source. Many of the larger dairy farms preserve extra colostrum by quick freezing in order that it will be available for other animals. When colostrum is not available, the young animal is frequently injected with whole blood from the dam. The purpose of this is to attempt to increase the antibody reserve of the newborn.

It has long been recognized that in general the young of one species thrive better on milk of their own kind than on that of another species. Furthermore, the sooner after birth the milk of another species is substituted for milk of the same species, the more unfavorable is the outlook for the young animal. The results of some studies published by Bilek are cited as indicating that some of the unfavorable effects so often obtained from feeding milk of another species may well be attributed to qualitative rather than quantitative differences. In these experiments, cow's milk and goat's milk were fed to the young of several species. The different species did not react alike. Kids used both milks equally well, while calves reacted to goat's milk with severe gastrointestinal disturbances which lasted as long as goat's milk feeding continued. Pigs showed no disturbance on cow's milk but reacted to goat's milk in a fashion similar to that observed in the calves. Foals showed a stubborn diarrhea when fed undiluted cow's milk but not the slightest disturbance on goat's milk. Since the two milks are very similar in percentage composition, the results indicate the presence in the milk of substances incompatible or toxic to the animals that reacted unfavorably. It is suggested that the incompatible factors are proteins.

It is known that the presence of a foreign protein undigested in the circulating blood is more or less toxic to an animal and may produce a sensitization to further additions of the foreign protein. It has been established that the newborn animal normally absorbs considerable protein undigested through the gastrointestinal wall. Although this apparent permeability decreased rapidly after birth, it probably does not cease abruptly, since as Ratner has shown, it still occurs to some slight extent in about 50 per cent of adults. The possibility of the absorption in the very young suckling of appreciable amounts of undigested and sensitizing foreign protein might be a major factor in the incompatibility of the milk of one species for the young of another.[1]

The young of all species will be better off if they are allowed to suckle for at least 3 or 4 days. After this, they can be hand-fed if desired, although this is seldom practiced except with dairy calves. Many sys-

[1] Earle, I. P., Food and Life, *U.S. Dept. Agr. Yearbook*, 1939, p. 508.

tems of feeding dairy calves have been devised and are available in various books and bulletins.

Colts, calves, lambs, kids, and pigs will begin to nibble at the dam's feed in from 2 to 4 weeks after birth. They should then be supplied with suitable fine roughage and with suitable grain mixtures, preferably in a creep to which the dam does not have access. For colts, a mixture of 2 parts cracked corn, 4 parts crushed oats, 2 parts bran, and 1 part linseed-oil meal by weight has been found to give good results. For calves, many starters and meals have been developed and are available under trade names. They can also be home-mixed from such ingredients as corn meal, ground oats, bran, middlings, and linseed-oil meal. Similar starters or home-mixed rations will also serve for lambs and kids. Pigs may also be fed home-mixed rations of corn, middlings, and protein supplements such as fish meal or tankage. Pigs should also be supplied a mineral mixture such as bone meal, 38 parts; calcium carbonate, 39; sodium chloride, 20; ferrous sulphate, 2.5; copper sulphate, 0.25; and potassium iodide, 0.03 parts by weight. In order to prevent anemia in pigs, many breeders paint the sow's udder daily with a solution of iron and copper or place fresh clean sod or dirt where the little pigs can get it.

For maximum growth and well-being the young must be comfortably housed in sanitary, safe quarters and must be properly fed both by their mothers and through their own efforts. To keep young animals on feed and gaining steadily from the day of birth is an art, gained only through experience. For maximum eventual returns, proper care and nutrition are indispensable. Any young animals do best if fed regularly, often, and moderately. They should clean up their feed with a relish and look for more, the secret of success being to keep them a little hungry. Misguided kindness in the form of too much feed must be avoided.

If the young are ever to achieve the maximum of their inherent capabilities, they must get started early along the proper path and must be kept moving. Normal healthy parents are the first prerequisite, clean maternity stalls the second, proper feeding and management of the lactating female the third. The young themselves will soon (1 to 3 weeks) evidence a desire to eat something besides milk. This desire should be satisfied not with shavings and sawdust but with good pasturage, fine-quality hay, and a suitable grain mixture. Remember that whole milk, and more especially skim milk, is very high in protein. Along with a suitable quantity and quality of milk from the dam and such other feeds as just mentioned should go a sufficient amount of exercise, preferably at pasture and in the sunshine.

Constructive breeding implies that records are to be kept. With the young animal this starts at birth. Among other things, the record should

show the animal's sire and dam, the length of gestation, the character of parturition (normal or otherwise), single or multiple births, weight of the offspring, their general condition, number born weak or dead, and any other pertinent data which will be of service when the breeder is deciding whether or not to breed the dam again or whether or not to save her offspring for breeding purposes. Parturition is a busy time for the herdsman, so that if he does not get his records then and there, they are likely never to be secured.

If the animals are to be marked in any way, it should be done early and before there is any chance of making mistakes. Pigs are usually marked by notching the ears; *e.g.*, a notch in the outer edge of right ear stands for 1, outer edge of left ear for 3, inner edge of right ear for 10, and inner edge of left ear for 30. Lambs and calves are best marked by metal tags, or calves by tattooing. If the tattoo fades, it can be made permanent in the other ear at about two years of age.

Complications before Parturition.—Many complications can arise during gestation that will interfere with normal parturition. Extra-uterine pregnancies have been known to occur in the ovaries, abdominal cavity, Fallopian tubes, the cervix, or the vagina. In human medicine these are usually recognized and are then removed by surgery. In farm animals they are not readily detected in their early stages and may terminate fatally or eventually become aborted or mummified.

Superfetation, the establishment of a second pregnancy in an animal already pregnant, sometimes occurs. This is not so common as is thought. The fact that twins or litter mates may be of unequal size does not indicate superfetation but rather that differences in physical development occur. Other instances of true superfetation may not be recognized because the second fetus conceived may be expelled at the time of parturition of the first fetus without arousing suspicion. However, there are authentic cases in which animals have given birth to normal young conceived and born at distinctly different times and not at two normally spaced periods.

Numerous developmental abnormalities have been observed. These are of many types and probably have many causes. Many of these abnormalities are confined to certain organs, *e.g.*, cleft palate, imperforate anus, etc., and do not interfere with parturition. In other cases fetal monsters (teratoma) in the form of unorganized tissue containing skin, hair, teeth, nervous tissue may develop.

In the human there are numerous diseases and functional disturbances which have either a direct or indirect effect on the course of pregnancy. The farm animals are not subject to many of these. The common genital diseases have been discussed in another section and will be only

mentioned here. Brucellosis may result in abortion in cattle, swine, and goats. In cows, a microorganism, *Trichomonas fetus*, may cause abortion. Abortions due to *Salmonella* and virus infections have been reported in mares, and in sheep and cattle *Vibrio fetus* has been associated with abortion.

Gross nutritional deficiencies as a cause of gestational difficulties are not common in the major livestock-producing areas of the United States. Of the specific nutritional factors which affect embryonic development, vitamin-A and iodine deficiency are the most common. In the female gross vitamin-A deficiency may be associated with abnormal embryonic development and abortion. Clinical iodine deficiency is more likely to occur in ewes and sows than in cows or mares. It manifests itself by the birth of weak or dead young with enlarged thyroid glands and considerable edema (watery infiltration) of the skin. Hairlessness or woollessness may occur.

One of the most spectacular complications of gestation is pregnancy disease of sheep. This is not a transmissible disease but a metabolic disturbance. Affected ewes first appear listless, refuse feed, and become progressively weaker. Within 1 or 2 days they become unable to stand and for this reason the term *parturient paralysis* is used. The condition usually appears in the last month of pregnancy, and ewes carrying twins or triplets are most apt to be affected. About 90 per cent of affected animals die. The condition is thought to be due to poor feeding and lack of exercise.

Accidents caused by slipping, crowding through narrow doors or gates, fighting, or general mismanagement may cause death or premature expulsion of the fetus.

Complications at Parturition.—Parturition may be complicated by anatomical abnormalities of the dam or fetus, malpresentation, muscular exhaustion, or extreme excitation of the dam. The proper physical condition of the female as parturition approaches and her confidence in the herdsman will do much to facilitate the process.

Difficult labor is called *dystocia* and its correction calls for experience and skill. The interference of an inexperienced person in a truly abnormal delivery is very apt to result in death of the fetus and serious injury or death of the dam. Perforation of the uterine wall by the feet is almost sure to be followed by peritonitis. Pulling when pushing is called for is apt to tear the genital organs or cause prolapse of the uterus or rectum. The skilled obstetrician seldom resorts to strength alone. If the problem is one of malpresentation, it is frequently most successfully met by first administering a local or general anesthetic. If a Caesarean operation is to be performed, it should be done before the animal is

exhausted or injured. In those rare instances when the fetus must be dismembered in utero, only the most experienced should be allowed to perform the task.

The breeder of valuable animals is concerned not only with the loss of one offspring, or litter, but with the lifetime breeding performance of the dam. Parturient injury followed by sterility is an expensive price to pay for carelessness or ignorance. We urge, therefore that no time be lost in securing a skilled veterinary obstetrician when conditions appear to be abnormal.

Complications Following Parturition.—The strain involved in parturition plus the avenues of infection that are automatically opened by it render the dam particularly susceptible to complications following parturition. They may take many forms, from retained placenta, hemorrhage, eversion of the vagina, uterus, or bladder, to lesions in various parts of the genital tract or the invasion of the tract by various organisms, causing inflammation of the uterus, cervix, or vagina, often accompanied by the formation of pus. In addition, milk fever, septicemia, paralysis, convulsions, and many other abnormal or diseased conditions may follow parturition. Surely the lot of the dam at this time is not an enviable one. The least the livestock breeder can do is to use all the precautionary measures regarding feed, care, and sanitation he can lay hold of and not begrudge or delay too long in getting the best skilled attention he can secure whenever it becomes necessary to have it.

Summary.—In this chapter we have discussed the role of hormones in the establishment and maintenance of pregnancy, and the causes and processes of parturition. Understanding something of the complicated process should make us, as livestock breeders, a bit more appreciative of the dam's situation during this critical time. With intelligent care and forethought, most of our animals can be brought through parturition unscathed and their offspring gotten off to a good start on the road to their eventual service in production or reproduction. We have seen that the process of parturition is often beset with a multitude of complications. If we are going to succeed in livestock breeding, we must learn to handle our animals intelligently at this time—the time and process on which the whole structure of animal breeding ultimately rests, for it has to do with the safe induction into the world of the animals that we hope our genetic planning and selection have given a good chance of being superior to their forebears.

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CHAPTER IX

MAMMARY DEVELOPMENT AND THE INITIATION OF LACTATION

The mammary glands are, to the zoologist, the distinguishing characteristic of all mammals; to the physiologist, an integral part of the female reproductive system; and to the dairyman, practically a way of life. There are wide differences between mammals in the anatomy and physiology of the mammary system. These range from the egg-laying mammals, such as the duckbill platypus in which the young scoop up the milk as it exudes from nippleless mammary areas, to the highly developed cow producing in excess of 30,000 lb. of milk annually without ever seeing her calf or its sire (if artificial insemination is practiced).

Embryological and Fetal Development.—The mammary glands are generally regarded as modified sweat glands. They originate as integumentary ingrowths in both sexes, but as fetal development progresses, the rate of mammary differentiation is more rapid in the female. In cattle the first evidence of mammary development is the appearance of a band of cells on the ventral surface of the embryo posterior to the umbilicus. The single band of cells soon divides into two parallel bands, and on each band two budlike areas of cells appear. Each mammary bud undergoes rapid growth and soon differentiates into a teat. In cattle there are ordinarily 4 mammary glands and 4 functional teats. In other species the number of teats and glands characteristic of the animal are proliferated along the mammary bands. The outstanding features of fetal development are the development of a canal in the teat (the teat cistern), a larger cavity at the base of the teat (the gland cistern), and a few ducts leading away from the gland cistern. These structures will later give rise to the duct system of the udder.

Prepubertal Development.—The functional mammary gland will contain connective tissue, fat, a duct system, a lobule-alveolar system, and large numbers of blood and lymph vessels, nerves, and smooth muscle cells. The period from birth to puberty is chiefly a period of increased connective tissue and fat deposition. The udder does increase somewhat in size, and there is a suggestion as to its future shape, but the amount of duct growth is very limited. In dairy cattle Swett and Matthews (1935 and 1942) reported that there is greater duct growth in calves which later

prove to be high producers than that in low producers. However, the limitations of a gross examination for the estimation of future microscopic changes make it difficult to estimate the probable eventual output of the mammary glands.

Postpubertal Development.—There are marked species differences in the extent of mammary development of the sexually mature but nonpregnant female. Such factors as length of the estrual cycle, function of the corpus luteum, and seasonal breeding patterns all contribute to the differences. In the mouse, which has a cycle of 4 to 6 days, there is marked duct growth until about 70 days of age but little further duct growth from 70 to 100 days unless pregnancy is established (Gardner and Strong, 1935). In the cow, which has an estrual cycle of 18 to 21 days, development of the duct system begins at puberty and continues more or less rhythmically prior to conception (C. W. Turner, 1939). There is more complete mammary development in the human prior to pregnancy than in other mammals. Duct growth is very extensive, and there is some evidence that alveolar proliferation may occur (C. D. Turner, 1948).

Mammary Changes during Pregnancy.—In most mammals the first half of pregnancy is devoted to the completion of the mammary duct system and the proliferation, at the extremities of the ducts, of the lobule-alveolar system. The chief purpose of the ducts is to transport the milk. The true secretory function of the udder is carried on by the secretory epithelium of the alveoli. Thus, anatomically at least, the mammary system is prepared for lactation by the mid-point of pregnancy.

During the last half of gestation there is an enlargement of the alveolar epithelium, and the lumina and ducts become distended with secretion. As parturition approaches, the degree of distension becomes greater and the udder may be extremely congested. The fact that the udder does not increase in size noticeably until the latter part of pregnancy led to the belief that maximum mammary growth occurs at this time. It is now clear that cellular proliferation characterizes the first part of gestation and cellular hypertrophy and secretion the latter part.

As previously discussed, abortion or proper mechanical stimulation is usually followed by milk secretion after the middle of pregnancy. The failure of animals to reach high levels of production in such cases is probably attributable to insufficient hormonal stimulation for secretion rather than incomplete anatomical development of the gland.

Mammary Involution.—Although the udder is regarded as a highly efficient organ, it does not function at maximum capacity for long. In fact, it requires from 2 to 4 weeks for a cow to reach maximum productivity, and no sooner is the peak reached than decline begins. This would be explained in nature on the basis of the needs of the calf. But by selec-

tion, the cow (or man) has achieved a level of secretion far in excess of the calf's requirements. The decline in secretion is the result of wear and tear on the mammary system (involution) and changes in hormonal and nutritional relationships. In fact, anything which affects the well-being of the cow will be reflected in mammary performance. As lactation progresses, the numbers of actively secreting epithelial cells and their degree of activity decline. The microscopic appearance of the udder of the dry, nonpregnant cow is very similar to that of the virgin. The reestablishment of pregnancy is necessary to stimulate both mammary growth and secretion in such an individual.

Endocrine Regulation of Mammary Development.—There is rather general agreement as to the cellular changes which occur as the mammary glands develop. It is true that there are wide species differences in the rate and type of development, but competent anatomists agree as to the structures which are present at particular times in the various species. However, there are few body systems whose functions have been explained by as many different theories as the mammary glands.

During the nineteenth century, when the nervous system was recognized as the chief coordinating agency of the body, it was believed that both the development and function of the mammary glands were under nervous control and that there were nervous pathways between the uterus and the mammary glands. This was disproved by such procedures as the severance of the central or peripheral nerves and finally by the grafting of mammary tissue to other parts of the body. The development and function of such grafts clearly showed that the nervous system was not a primary regulator of the mammae.

It had long been known that sexual maturity was followed by some mammary growth in most species and that final development and milk secretion were dependent upon pregnancy and parturition. The discovery that the ovary was both an endocrine and gametogenic organ soon led to the conclusion that the mammary glands were under endocrine control. The exact nature of the endocrine mechanisms involved is not yet agreed upon.

As cited by Trentin and Turner (1948), Allen *et al.*, Laqueur *et al.*, and Turner and Frank showed that the estrogenic hormone prepared from follicular fluid would cause development of the mammary duct system. It was then found that corpus luteum extracts in combination with estrogens would induce alveolar growth. As a result of these studies, it was concluded that estrogen was responsible for mammary duct growth and that progesterone, preceded by estrogen, resulted in the proliferation of the alveolar system. It was recognized, however, that complete mammary development could be induced in the guinea pig with estrogen alone.

Simultaneously with the studies being carried out on the physiological effects and chemical nature of the ovarian hormones, it was reported that anterior pituitary extracts or preparations would induce mammary growth in castrate and hypophysectomized rats (Asdell, 1931; Nelson and Pfiffner, 1931, and others). In 1937, Gomez, Turner, and Reece found that the anterior pituitary glands of estrogen-injected rats would stimulate mammary growth in hypophysectomized guinea pigs, lending support to the theory that the anterior pituitary secretes specific mammary-growth-stimulating hormones. A new theory was developed in which duct growth was accounted for by the secretion of the mammogenic duct growth factor, and lobule-alveolar development was attributed to a second anterior pituitary mammogenic hormone (Gomez and Turner, 1937, 1938).

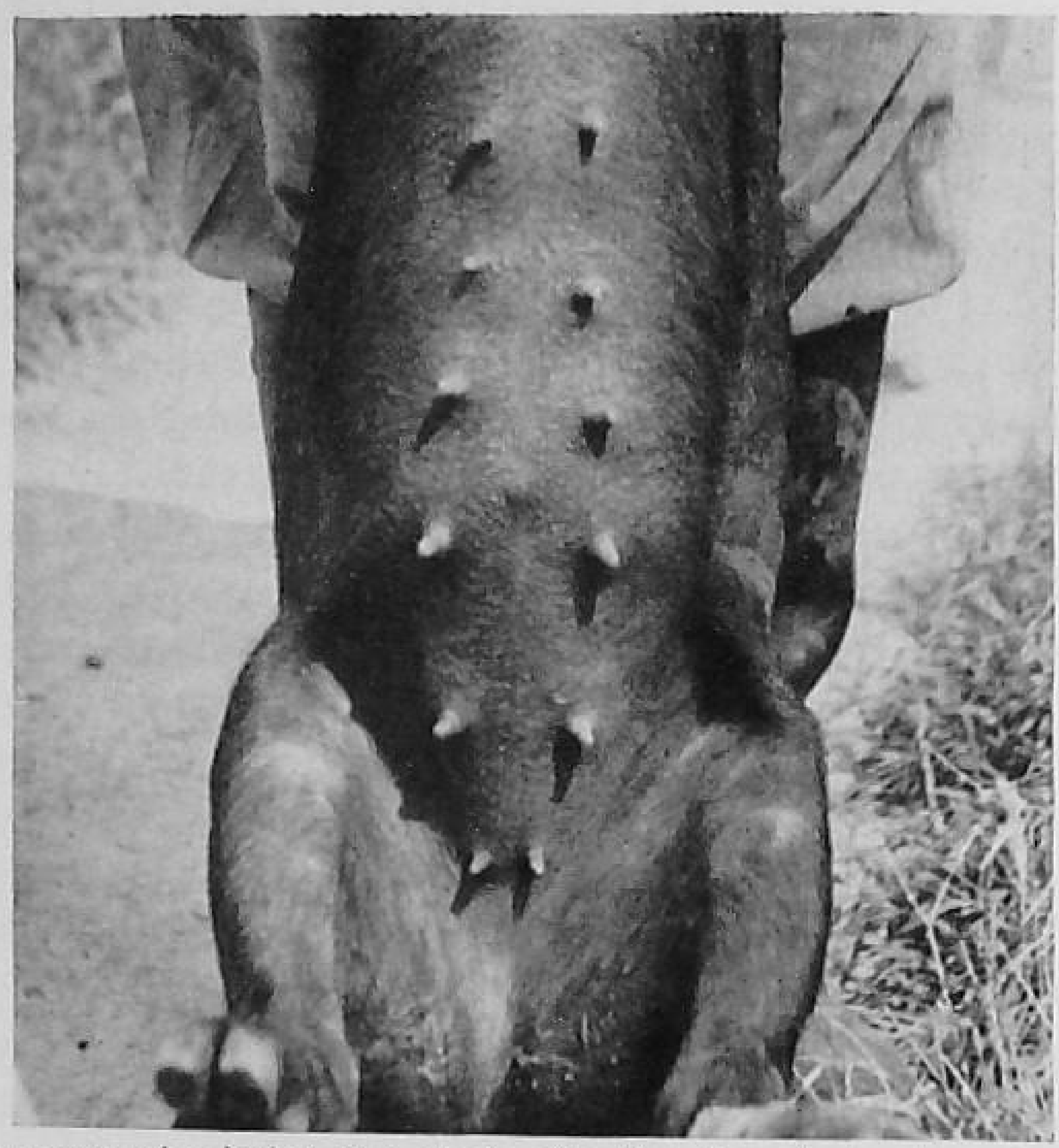

FIG. 76.—Mammary stimulation of a virgin gilt after 3 weeks treatment with stilbestrol resembles that of mid-pregnancy.

Agreement has not yet been reached as to whether estrogen and progesterone act directly upon the mammary gland, causing (1) duct growth, and (2) lobule-alveolar differentiation, or whether these hormones stimulate the anterior pituitary gland which in turn causes mammary development.

In the normal guinea pig and goat, and to some extent in the human and monkey, estrogen alone induces duct and lobule-alveolar growth

(C. D. Turner, 1948). In cattle the natural estrogens produce only duct growth, but stilbestrol, a synthetic estrogen which has not been found in nature, induces complete mammary development and sometimes copious lactation (Espe, 1946).

The present status of the mammogen theory was summarized by Trentin and Turner in 1948. It was concluded that the active pituitary factor is associated with the protein fraction rather than with the lipid soluble fraction as previously reported. It was further concluded that the present evidence does not warrant the conclusion that there are two separate mammogens, but that they should be considered as the same pituitary factor. In an extensive series of studies of mammary development of the male mouse, these authors found that continued estrogen injection caused marked duct growth and some alveolar development in normal male mice. Combined estrogen and progesterone treatment was much more effective than either hormone alone at the same dosage. However, when the pituitary glands of male mice were removed, estrogen produced little mammary growth and a combination of estrogen and progesterone resulted in slight duct growth (Trentin and Turner).

Thus, in 1949, there are at least two distinct theories for mammary development. One of the most serious criticisms of the mammogen theory is the fact that percutaneously applied estrogens have been shown to have limited local effects when applied to single mammary glands in mice, rabbits, monkeys, and other animals. In other words, the application of estrogen to one gland does not affect neighboring glands. If the effects of estrogen were through the pituitary, all glands would be expected to respond (C. D. Turner, 1948).

A wide variety of substances has been shown to either directly or indirectly affect mammary growth. Extensive stimulation has been obtained in normal and castrate male and female rats following androgen administration. In the human male enlargement and tenderness of the mammae are not uncommon at puberty. Extensive mammary development and lactation can be induced in males by appropriate hormone treatment, and it is not uncommon for considerable milk secretion to occur spontaneously in male goats. Abnormal mammary growth, including cancer, is one of the serious problems in human medicine. The exact cause remains as yet obscure, but several chemical substances which will induce experimental carcinogenesis are known.

THE INITIATION AND MAINTENANCE OF LACTATION

The Lactogenic Hormone.—The hormone responsible for the actual initiation of milk secretion following the anatomical development of the mammary gland was discovered by Stricker and Grüeter in 1928.

These French physiologists found that anterior pituitary extracts would induce milk secretion in pseudopregnant rabbits and later showed that such extracts would bring about milk secretion in dogs, cows, and swine if the mammae were properly developed. The specific anterior pituitary hormone responsible for the initiation of lactation has been called *galactin*, *prolactin*, and the *lactogenic hormone*. The last two names are in wide general use.

The lactogenic hormone has been isolated from the anterior pituitary gland in rather pure form. It is a protein with a molecular weight between 22,000 and 32,000 and because of this fact is not likely to be synthesized in the near future.

This hormone has a rather wide variety of effects in different species. In pigeons it stimulates the secretion of crop milk, depresses ovarian and testicular activity, will induce broody behavior, increases metabolic rate, and even stimulates growth of the intestinal tract. In mammals the lactogenic hormone is primarily concerned with the initiation and maintenance of milk secretion, but it may likewise play some part in parental instinct.

It is well known that the lactogenic hormone exerts its greatest effect shortly after parturition and that the lactogen secretion of the anterior pituitary declines as lactation progresses. It has been shown that dairy-cattle pituitaries contain more of the hormone than those of beef cattle and that pregnant cows have more than do calves (Reece and Turner, 1937). The factors which are involved in the actual initiation of lactation and its maintenance at optimum levels have recently been reinvestigated by Meites and Turner (1948).

Determinations of the lactogenic hormone content of the anterior pituitary glands of various species have shown that it is present in only small amounts during pregnancy, increases slightly shortly before parturition, and is secreted in large amounts immediately following parturition. It has been shown that the injection of estrogen is followed by a marked increase in pituitary lactogen but that when progesterone is administered simultaneously the pituitary response is inhibited. As previously described, both estrogen and progesterone are secreted during pregnancy. It is believed that progesterone is dominant over the estrogen during most of pregnancy but that at the approximate time of parturition estrogen becomes dominant, the lactogenic hormone is secreted by the anterior pituitary in increased amounts, and lactation is initiated (Meites and Turner, 1948).

The maintenance of a high rate of milk secretion following parturition is of great concern to dairymen, and, for that matter, to the producers of all farm mammals. The most outstanding dairy cows are persistent milk

producers. The rate of decline of lactation is slow by comparison with the average or inferior cow. It appears logical to assume that the rate of decline is in some way related to the level of secretion of the lactogenic hormone. The correctness of this assumption has been borne out by experimental evidence, but the exact nature of the controlling mechanisms is not wholly understood.

It is well known that the removal of milk from the mammary glands is quickly followed by the secretion of more milk. If milk is not withdrawn, involution of the udder sets in. It has been shown that the suckling stimulus increases the secretion and discharge of the lactogenic hormone by the pituitary and assists in the maintenance of the mammary gland in a functional condition (Meites and Turner, 1943).

Other Hormones.—Milk secretion is a complex function requiring the cooperation and coordination of all the body organs and systems. High milk production cannot be attributed to any one factor, such as mammary size, level of lactogen secretion, feed capacity, nutritional status, or a single gene.

Of the hormones other than estrogen, progesterone, and the lactogenic hormone, those of the thyroid and adrenal glands are probably next in importance.

The thyroid gland, through the mediation of its hormone thyroxine, is chiefly concerned with the regulation of general body metabolism. The removal of the thyroid in the lactating animal is followed by a rapid drop in milk production. In contrast, the administration of thyroxine during the declining phase of lactation is frequently followed by increased milk production and an increase in the fat content of the milk. The discovery of a relatively simple method of producing thyroxine by the iodination of casein has led to extensive studies regarding the possibility of increasing milk production by the feeding of such thyroidally active compounds (Reineke and Turner, 1942). Iodinated casein is usually referred to as a thyroprotein and has been shown to contain about 3 per cent thyroxine. The place of thyroprotein in practical milk production is not yet clear. Experimentally, it has been shown that the addition of thyroprotein to the rations of dairy cattle during the declining phase of lactation may increase milk production as much as 20 per cent and butterfat production as much as 25 per cent for short periods of time. Many factors may affect the results. Some cows respond more than others, and some animals may not respond at all or even adversely. It must be recognized that thyroxine has a marked effect on the processes of metabolism and the circulatory and respiratory systems. Excessive stimulation is usually followed by considerable weight loss and eventually by decreased milk production. In cattle in which suboptimum thyroid activity is limiting

milk secretion, the judicious use of thyroprotein would seem to offer possibilities for increased production.

The adrenal cortex (outer portion of the adrenal gland) is ordinarily regarded as essential for the maintenance of life itself. It is not surprising, therefore, that the removal of the adrenals in a lactating animal is followed by the cessation of lactation. The hormone, or hormones, secreted by the cortical cells are concerned with normal carbohydrate metabolism, the distribution of electrolytes, and normal kidney function. The interference with any of these functions could be expected to influence lactation.

The parathyroid glands are concerned with calcium and phosphorus metabolism and skeletal development and thus indirectly with skeletal muscle irritability and milk secretion. One of the most dramatic disorders of farm animals is milk fever in the cow. This condition is, in reality, not a fever, but hypocalcemia. It occurs almost exclusively in high-producing dairy cattle shortly after calving and is apparently the result of the greatly increased requirements of the lactating animal for calcium. It is a very serious metabolic disturbance and may result in death unless prompt treatment is given. The original treatment for the condition, the inflation of the udder with sterile air, succeeded because the air pressure thus created inhibited milk secretion and gave the animal time to adjust its calcium metabolism. The presently recommended treatment is the intravenous administration of both calcium and glucose. Although the basic cause is not completely known, it is thought that the parathyroid glands are involved.

The Ejection or "Let Down" of Milk.—During the nineteenth century it was generally believed that the greater part of the milk was secreted during the milking process as the result of the nervous stimulus produced by manipulating the udder. This view is still widely held by dairymen. As the result of improved techniques for studying the factors affecting milk secretion, it is now definitely known that nearly all of the milk is present in the udder prior to milking. It has likewise been established that milk is secreted most rapidly immediately after milking when the udder is empty. As the udder fills with milk, the pressure within the ducts and alveoli increases and results in decreased secretion. As previously explained, the pressure which is developed in the udder by the introduction of air in the treatment of milk fever effectively stops the secretion of additional milk. Every dairyman knows that the most effective way to dry off a cow is to stop milking her, although he sometimes hesitates to do so for fear of injuring the udder.

Occasionally a cow does not produce the expected amount of milk at a particular milking, although the udder appears to contain more. Under

these conditions it is frequently said that the animal has "held up" her milk. This is very annoying to the practical dairyman, and he has been known to resort to various drastic measures to make the cow "let down" her milk. Most of these measures are ineffective because they are in opposition to the physiological principles involved.

We know now that a cow cannot "hold up" her milk but that she can fail to "let it down."

The greater part of the milk secreted is stored in the millions of alveoli which make up the secretory system. Small amounts of smooth muscle are associated with each alveolus, and it is necessary for these muscles to contract if milk is to be forced out into the large ducts.

This problem has been extensively investigated by Ely and Peterson (1941) and others, and it is now accepted that the "let down" of milk is a reflex act involving sensory nerves which stimulate the posterior pituitary gland which in turn secretes a hormone (the oxytocic factor) which stimulates the smooth muscles around the alveoli and results in the ejection of the milk.

The production of maximum quantities of milk requires that the milk be removed from the udder as soon as possible after the hormonal "let-down" stimulus has been given. These principles are being widely employed by dairymen and are the basis for the various techniques of "fast milking" which are being advocated. The natural "let-down" stimulus is, without much doubt, the crying of the young and the suckling act. Dairy cattle have come to associate many other stimuli with milking. Such factors as bringing the animals from pasture, the rattling of milking machines, movements of feed trucks, washing the udder, or even radio programs which the milkers tune in, stimulate the posterior pituitary and cause milk ejection. The normal stimulus may be easily interfered with. Changes in the animals' routine, strange noises or animals in the barn, mistreatment of the cattle, etc., may prevent the normal pituitary response. Ely and Peterson (1941) reported that events which frighten or disturb cattle probably cause the central portion of the adrenal gland (medulla) to secrete adrenalin, which in turn inhibits the normal action of oxytocin on the muscles surrounding the alveoli. There is considerable evidence available in a wide variety of species that fright or emotional stress results in the almost instantaneous release of epinephrine (adrenalin) into the blood stream.

From the practical standpoint it appears that the hormonal stimulus for "let down" sometimes is lost before milking is completed. If, for example, a cow associates the washing of the udder with immediate milking, delay in milking may result in decreased production. Experiments in which the oxytocic hormone has been injected showed that its

effects disappear in about 10 minutes. The understanding of the processes of milk secretion and ejection are of considerable importance in dairying.

Summary.—We have considered the mammary glands as an integral part of the female reproductive system. Relatively little mammary development occurs prior to puberty. After the establishment of ovarian function there is, in most species, growth of the mammary duct system. Although there are some species differences, the development of the lobule-alveolar system, the secretory portion of the gland, awaits the establishment of pregnancy. During the first half of pregnancy the alveolar tissue is formed and the gland is anatomically ready for secretion. There is a difference of opinion as to the exact means of hormonal regulation of mammary development, but it is clear that estrogens and progesterone are both involved. Whether these substances act directly on the mammary gland or through the anterior pituitary is not agreed upon. The udder appears to grow rapidly during the latter part of pregnancy, but we now know that this is the result of the distention of the gland with secretion. The active secretion of the mammae awaits the production of the anterior pituitary hormone, lactogen or prolactin. This hormone is usually secreted in maximum amounts shortly after parturition. Even though the mammary glands may be fully developed and in active secretion, the animal must be in a proper physiologic or psychologic state for the ejection, or "let down," of the milk. This process is now regarded as a reflex act involving sensory nerves which cause the posterior pituitary to produce oxytocin, which in turn brings about the contraction of smooth muscle cells in association with the alveoli and forces the milk into the duct system, where it can be easily removed by the young or by the milking act.

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CHAPTER X

ARTIFICIAL INSEMINATION

Few advances in methods of livestock production have been so rapidly and enthusiastically accepted as the artificial insemination of dairy cattle. Not that the technique is limited only to dairy cattle, but economic and management conditions have made it especially adaptable to this class of animals in the United States. There are certain situations which make it equally valuable in sheep, swine, horses, chickens, fur bearers, and even the human.

By definition, artificial insemination is the deposition of spermatozoa in the female genitalia by instruments rather than by natural service. The term *artificial breeding*, which is now widely used to describe the process, has in the past suggested something unnatural or even repugnant to livestock owners. To some it has meant the solution of all breeding difficulties, the possibility of impregnating the entire herd at one time, or the regulation of sex. To others it has suggested that the offspring might be weak or otherwise abnormal, and many farmers traveled for miles to observe the first calves born as the result of artificial insemination. When properly employed, artificial insemination has little effect on normal breeding efficiency. There are rare instances of animals with abnormalities preventing normal breeding which have conceived following artificial insemination, and there are numerous instances in which the improper use of the technique has failed to bring about pregnancy. It can be accepted as a fundamental breeding principle that females which cannot conceive following service to a normal male will not perform any better when artificially inseminated.

History of Artificial Insemination.—Artificial insemination is not new. Loessl (1934) relates a supposedly authentic account of an Arab chief in 1322 who mated a prized mare with the stallion of an enemy chieftain by stealthily collecting semen from the stallion's sheath and successfully artificially impregnating his mare. It is definitely known that Spallanzani was successful in the artificial insemination of dogs in 1780, and Hunter (1799) produced a pregnancy in the human by this method. Iwanoff, a Russian physiologist, began a study of artificial insemination in farm animals as early as 1899, established a laboratory for further investigation in 1909, and initiated large-scale investigations and the practical application of the findings in 1922.

One hesitates to trace the development of artificial insemination in the United States, for this technique has undoubtedly been discovered and rediscovered numerous times. In 1906 Lewis, at the Oklahoma Station, described the use of the impregnator for the insemination of mares and in 1911 wrote "the use of the impregnator, or other artificial means of introducing the semen, in horse breeding has passed beyond the experimental stage." Yet, in 1949, we are still careful to assure cattlemen that this technique has now passed beyond the experimental stage.

The first large-scale artificial-insemination association in the United States was organized in Clinton, N.J., in May, 1938, by Prof. E. J. Perry of the Dairy Extension Service, and similar organizations were established in several other states in 1938 and 1939. There is probably not a single state which does not have at least limited artificial insemination available. Statistics released by the Bureau of Dairy Industry as of Jan. 1, 1949, showed that in the United States there are 1,263 artificial-breeding cooperatives with a membership of 316,177 and 2,412,160 cows listed for insemination. When the third edition of this text was published in 1942, it was estimated that about 100,000 dairy cattle had been inseminated the previous year.

ADVANTAGES OF ARTIFICIAL INSEMINATION

Increased Use of Proved Sires.—The greatest advantage of this method of breeding is that it has increased the usefulness of superior sires. In previous chapters we have made recommendations regarding the frequency of use of males. It is a rare bull that is naturally mated to as many as 50 or 60 cows a year and even more rare for one to sire as many as 200 calves during a lifetime. Milkdale Aristocrat Rag Apple, one of the great Holstein bulls of his time, sired more than 10,000 calves in the New York Artificial Breeders' Cooperative. It would have taken him about 200 years to accomplish this in natural service. But the real value of such a bull is in his ability to transmit high milk production to his offspring. The first 10 tested daughters of this bull produced 664 lb. of milk and 46 lb. of butterfat more than their dams, and the dams themselves averaged more than 500 lb. of butterfat.

Adequate records are now available to prove what animal geneticists have predicted. For the United States as a whole, the cows born as the result of artificial insemination have produced 859 lb. of milk and 41 lb. of butterfat more than their dams (Lawritson and Nibler, 1946). These increases are similar to those reported by states such as New York and New Jersey which have been in the program the longest.

In areas where the levels of production of the cows are not so high as

in the intensive dairy states, the improvement of the daughters should be even more striking. In Indiana, for example, the average milk production is about 4,200 lb. and fat yield about 190 lb. The use of proved sires with average indexes of 500 lb. of fat should have a profound effect on the productivity of the daughters in this case. We cannot assume that production will fall halfway between the index of the sire and the dam, for we do not yet know whether the owners of cows which produce 200 lb. of butterfat will make the adjustments in feeding and management which 350-lb. cows require. If butterfat production should be only half of that anticipated, the increase would still average 75 lb. There can be little question that the availability of the services of such proved sires at average fees of $7 per cow provides the average dairyman with germ plasm seldom if ever available to him before.

Allows More Sires to Be Proved.—There is no one answer to the question of whether only proved sires should be used for artificial insemination. If all other factors were equal, there is little doubt that we would select only those males which had been progeny-tested. The supply of proved sires has never been sufficient to meet the demand. The rapid increase in the use of artificial insemination has resulted in very keen competition for the good individuals which are available. As has been true in the past, many of the best males have gone to the slaughterhouse before their worth became known, and others are old and debilitated. Many of these proved sires have fairly satisfactory fertility when used in limited natural service but have not produced semen of the quality essential for artificial insemination.

It seems logical to expect that in the near future artificial-insemination associations must undertake some type of a proved-bull program. The chief risk to livestock owners in proving bulls is that they might end up with a group of replacement animals inferior to the parent stock. This risk could be distributed so widely by artificial insemination that even disappointing bulls would cause little loss to individual herd owners. If all members of local artificial-insemination associations bred a few cows to promising but untried young bulls, the risk would be negligible and the method of proof would be better than that now used. Instead of having 5 or 10 tested daughters, we could expect a sire to have perhaps 100 or more, and in addition the results would not be unduly influenced by conditions in a single herd.

Eliminates Need of Bull in Small Herds.—The owner of a small herd is faced with a great many problems in regard to the purchase and maintenance of a sire. He cannot afford to buy the quality of animal now available for artificial insemination. He likewise hesitates to build the

kind of quarters necessary for safety in keeping the bull, to say nothing of conditions which will be optimum for the maintenance of the male in good breeding condition. It has been shown that the actual cost of artificial insemination in herds of 10 cows or less is not so great as when a bull is kept. It is therefore safer and cheaper, and far superior from the breeding standpoint, for the smaller dairyman to adopt artificial insemination.

Lessens Disease and Improves Breeding Efficiency.—These advantages can likewise be possible disadvantages if artificial insemination is not properly used. The selection and care of the bulls used for artificial insemination must be in the hands of people who are specially trained for such work. When proper precautions are taken, the spread of genital diseases by the male should be virtually eliminated. The problem of reproductive disturbances in the female still is an important one. It appears that the interest which is being developed in the owners of artificially inseminated cows is already having its effect in the early detection and treatment of breeding difficulties. Improved systems of record keeping, plus the fact that every cow is closely observed during insemination, has been helpful in the early diagnosis of genital disturbances.

Miscellaneous Advantages.—Artificial insemination is often of value in overcoming certain nonheritable physical difficulties. It facilitates the mating of animals of greatly different size; it extends the usefulness of sires that for some reason may have become incapable of performing natural service; it increases the use of males of monogamous species such as the fox; and it promises to be a useful technique in hybridization experiments.

It usually results in the keeping of better calving and breeding records, and as previously mentioned, this is one of the prerequisites to better breeding efficiency.

Artificial insemination should result in the development of animals of more uniform type and production and thus attract livestock buyers to a community.

Perhaps one of the outstanding advantages of artificial insemination is that it has stimulated greater interest in better livestock-breeding and management practices. There is little pride of accomplishment in the production of mediocre and inefficient animals. Dairy-extension men and county agents have found the introduction of artificial insemination to be followed by increased interest in methods of raising calves, the feeding and care of pregnant cows, and in dairy-herd improvement associations.

DISADVANTAGES OF ARTIFICIAL INSEMINATION

There are no disadvantages of artificial insemination which cannot be overcome by the application of knowledge which is at present available. Artificial insemination will not overcome sterility or result in higher fertility than can be attained when normal healthy cows and bulls are mated. The careless use of artificial insemination will result in lowered breeding efficiency, and failure to follow strict sanitary practices may result in the spread of disease. These should not occur in a properly managed association.

The conception rate immediately following the establishment of an artificial-insemination association in a particular community is frequently lower than the previous natural-breeding efficiency. It appears that this is most frequently due to inexperience both on the part of inseminators and owners. The rapid acceptance of this method of breeding has resulted in a great shortage of trained inseminators. It should be recognized that even the best conducted insemination schools cannot turn out a finished product in 10 days or 2 weeks. The basic principles of insemination can be learned, but the development of an automatically smooth routine of insemination requires much practical experience. Most inseminators require experience with about 200 cows before they become highly proficient. The herd owners likewise need experience. The detection of heat, observations in regard to the exact onset and duration of heat, the necessity of calling insemination headquarters at certain agreed-upon times of day, having cows which are to be bred readily available for the inseminator, and cooperating in every way possible with the inseminator will do much to guarantee the success of the practice.

Some of the disadvantages or dangers which seemed important a decade ago have not materialized. As far as is known, unscrupulous operators have not misrepresented the source of semen used. The use of artificial insemination has not "ruined" the purebred breeder. If anything, the demand for *good* sires has increased. Some associations have failed, but the failures have usually been human ones rather than due to a lack of basic knowledge of how to make artificial insemination work.

METHODS OF COLLECTING SEMEN

The ideal method of collecting semen is, theoretically, one which is completely satisfactory to the male, which is easy to use, which requires a minimum of equipment, and which permits the collection of a sample of normally ejaculated semen free from contamination with dirt, bacteria, or secretions from the female genitalia. Many techniques have been

developed. Some methods are applicable only to certain species; others are too complicated in principle and practice; some do not result in the normal ejaculation of the male and the production of completely normal semen; and others yield semen that is diluted with vaginal and cervical secretions and often heavily laden with bacteria.

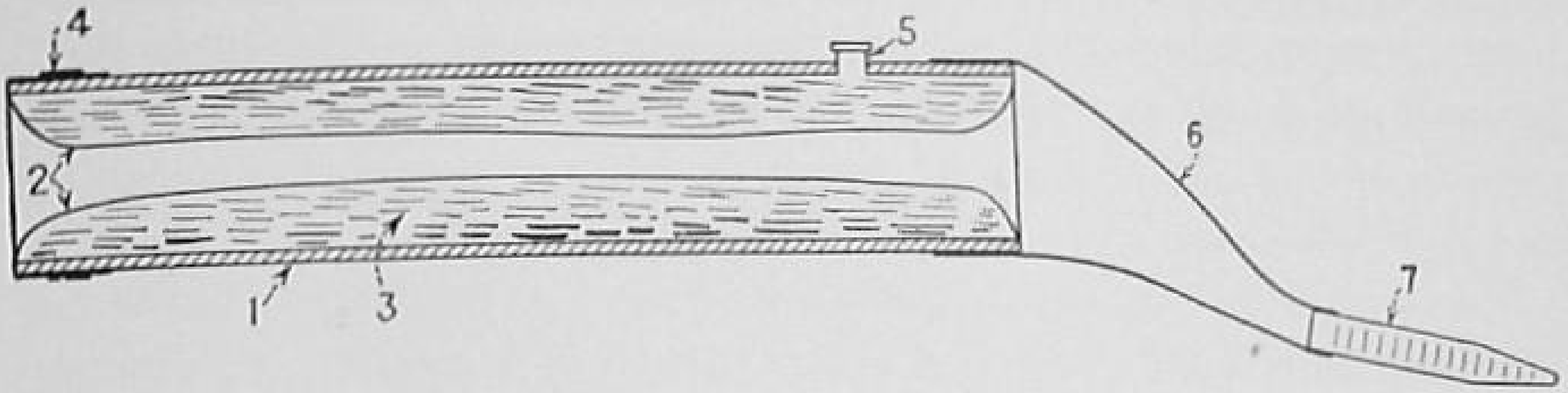

FIG. 77.—Diagrammatic artificial vagina for the collection of bull semen. 1. Outer rubber jacket. 2. Entrance for penis. 3. Warm water. 4. Heavy rubber band. 5. Water inlet. 6. Rubber cone. 7. Graduated test tube.

The Artificial Vagina.—During the past few years, Russian, British, and American laboratories have developed a type of apparatus called the *artificial vagina*. Its principle and construction, whether for bulls, boars, rams, or stallions, is simple, and it meets all the requirements of the ideal method. The apparatus is made up of an outer tube or casing,

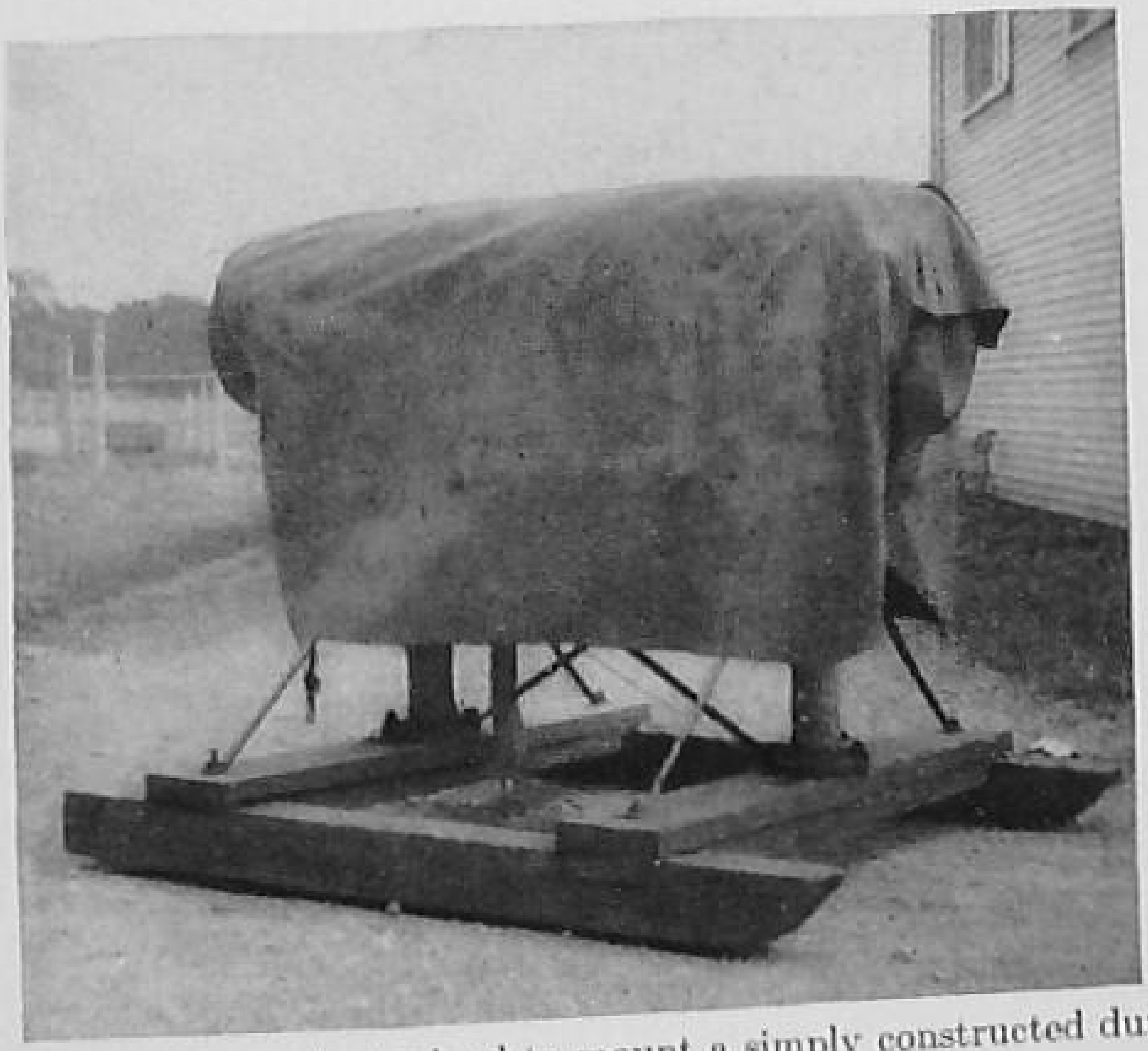

FIG. 78.—Bulls can be trained to mount a simply constructed dummy.

usually constructed of heavy rubber, metal, or one of the plastics, and an inner tube, or lining, of thin rubber. The space between the two tubes is usually filled with warm water or air or both; one end of the apparatus is open to allow the entrance of the penis and to the other end is attached a glass tube, or beaker, to catch the semen after ejaculation.

The success with which this method is used depends upon the skill of the operator and the training of the male, but most workers feel that it is the most satisfactory yet devised. The equipment should be clean, sterile, and dry before use. Males are very particular that the apparatus be of the correct temperature, pressure, and degree of lubrication, and conditions that suit one male may be unsatisfactory for a second. The proper temperature is attained by introducing warm water (40 to 45°C. for most males) between the outer and inner casings; the correct pressure

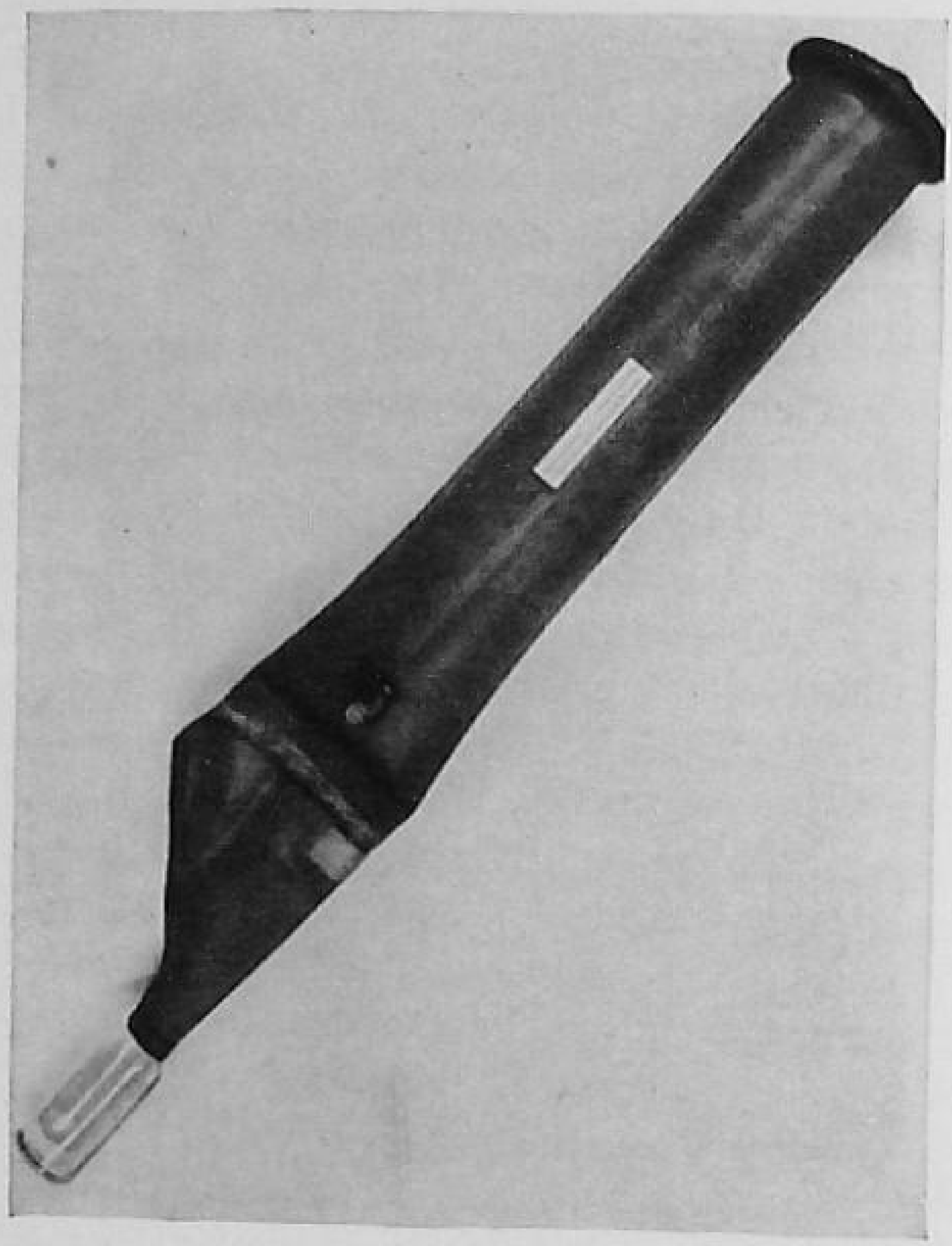

Fig. 79.—Artificial vagina for stallion.

depends largely upon the size of the penis of the male in question and is usually regulated by introducing or releasing air between the casings. A small amount of special lubricant, which is commercially available, should be applied to the first few inches of the inner rubber tube, but the amount used should be kept to a minimum, for it is undesirable to have any excess lubricant carried through the artificial vagina and mixed with the semen.

Males usually respond to this method without previous training. Best results are attained when the male is allowed to mount an estrus female and the penis quickly guided into the open end of the artificial

vagina. If the proper temperature, pressure, and degree of lubrication have been maintained, ejaculation is instantaneous in the bull and ram and is very shortly initiated in the stallion and boar. Active males may easily be trained to mount nonestrus cows, other males, or dummy females, and highly satisfactory samples of semen can quickly be collected.

The Massage Method.—Miller and Evans (1934) developed a technique of collecting semen from bulls by the massage of the ampullae of the vasa deferentia. The successful application of this method, which consists of the insertion of the arm into the rectum, the location and manipulation of the ampullae, seminal vesicles, and prostate region, and the collection of semen as it drips from the glans penis, requires a high degree of skill. It is most valuable for the collection of semen from bulls with injuries to their legs, backs, or reproductive organs, but for genetic reasons should probably not be applied to bulls suffering from physiological disturbances preventing service that might be transmissible. This method does not compare in usefulness with the artificial vagina. There are marked differences in the response of individual bulls; the semen is often contaminated as it drips from the glans penis; the volume and concentration of semen obtained by this method is often less than by service into an artificial vagina; and the mixture of urine with the semen at the time of collection often kills the spermatozoa.

Burrows and Quinn (1935) perfected a massage method for the collection of semen from the domestic fowl and turkey that is widely and successfully used. The copulatory organ of the male can be protruded by manipulating the cloacal region, and the semen stored in the bulbous ducts can be pressed out by the thumb and first finger.

Recovery of Semen from the Vagina.—One of the older methods of semen collection is the recovery of semen from the anterior vagina following natural service. This can be accomplished by introducing a glass or rubber catheter into the vagina, locating the pool of semen, and aspirating it into a syringe. This method can be used satisfactorily for the recovery of both ram and stallion semen if the genital health of the ewe or mare is known to be satisfactory. However, this method is not the one of choice in any species. Breeders who do not have other collecting equipment can make use of the method for the recovery of a semen sample for a fertility examination. The simplicity of the method is overbalanced by several disadvantages. The semen may be excessively diluted by female secretions and may have poor storage qualities. If an infectious genital disease is present, it is very apt to be spread to the inseminated animals.

The Breeder's Bag.—This technique, which involves placing a rubber sheath over the glans penis, has been satisfactorily employed by some

stallion and jack owners for many years and has been discarded by others as unsatisfactory. The chief criticism of the method has been that the bag often slipped from the penis as the male dismounted. This has now been overcome by the development of a longer type of sheath. The method has the advantages of simplicity and the recovery of a normal ejaculate, but is limited to equines.

Electrical Ejaculation.—This technique was developed by Gunn in 1936 as a method for the collection of ram semen. Various modifications have been made for small animals, and it has been of value from a research standpoint.

Two electrodes are used. In some species one is placed in the rectum and the other in the muscle above the loin, in other species one electrode is placed against the roof of the mouth and one at the base of the skull. An alternating current of varying intensity, depending on the species, is applied. The equipment is expensive, requires a high degree of skill, and gives variable results, even in experienced hands. It is unlikely that it will ever be widely used in practical semen collection.

THE EVALUATION OF SEMEN

The successful application of artificial insemination is, to a large extent, dependent upon the quality of semen used. Those responsible for the collection, processing, and shipment of semen must be able to evaluate its quality and to predict its potentialities when used under practical conditions. Those concerned with the insemination of cows must likewise be able to evaluate semen, lest females be inseminated with nonviable sperm.

Nearly every sperm physiologist is hopeful of being able to develop a *single* method of evaluating semen quality. The list of techniques which have been used is a long one and varies from the visual over-all score of semen following a brief microscopic view, to the chemical determination of enzymes, vitamins, or specific metabolic processes. Unfortunately no *one* method will yield an accurate estimate of the actual per cent of inseminations which will result in pregnancy when a particular semen sample is used. However, the fact that the conception rate does not fluctuate greatly between days or months or between well-managed insemination associations indicates that a fairly good job of evaluation is being done.

Volume of Semen.—Volume is usually determined in a graduated centrifuge tube in the bull, with a 1-ml. tuberculin syringe in the ram and rooster, and with a 100- to 200-ml. graduate in the stallion and boar. The volume is not necessarily related to the fertilizing capacity of the spermatozoa, since sterile animals may produce large ejaculates. Volume is of great practical importance in artificial insemination. If all other

factors in regard to quality are equal, the male with a large ejaculate is most desirable. The rate of semen dilution which will be made is determined largely on the basis of semen volume and numbers of sperm per unit volume of semen.

Number of Spermatozoa.—The number of spermatozoa per unit volume of semen varies with species and individual, and breeding males should be expected to meet the requirements for their species as previously elaborated. The number of sperm in semen is usually expressed in terms of sperm per cubic millimeter. The standard method of counting sperm is the same as that employed for counting red-blood cells. This technique is described in detail in nearly every physiology text. In brief, it involves the dilution of the semen in a red-blood cell diluting pipette, the thorough shaking of the pipette to bring about an even dispersion of the sperm, and the discharge of a small quantity of the diluted semen into the measured chamber of a hemacytometer. The number of sperm within certain ruled areas of the hemacytometer is counted beneath a microscope, this number is multiplied by a standard factor, and the number of sperm is thus determined.

Methods for the estimation of sperm numbers by the centrifugation of capillary tubes containing whole semen have been described. By centrifugation at a certain speed in relation to gravity for a standard time, the sperm are packed into one end of a capillary tube and the volume of the packed cells is measured. This method has the advantage that several replications of each sample can be made simultaneously, but it has not been used in practical insemination work (Shaffner and Andrews, 1943).

The ideal method of determining sperm numbers in bull studs must be simple, rapid, and accurate. It had been shown that the dilution of semen at a standard rate and then measuring the relative light transmission in a photoelectric colorimeter was rapid and accurate, but the equipment required was rather expensive (Comstock and Green, 1939). This method was adapted for field use by the development of opacity standards for the simple visual comparison of diluted semen. Complete directions for the preparation of standardized tubes of different opacity have been described by Salisbury *et al.* (1943). Such tubes are now available commercially. The equipment is called the comparator, is inexpensive and rapid, and is nearly as accurate as any other method. This is the standard technique of determining sperm concentration in most bull studs.

Motility of Spermatozoa.—The estimation of sperm motility by microscopic examination is one of the oldest of all clinical examinations involving the microscope. In fact, Leeuwenhoek, the father of microscopy,

and Dr. Ham described the appearance of spermatozoa in 1677. This estimation of semen quality has many limitations, but is probably the one most used by those engaged in practical artificial insemination.

As discussed in an earlier chapter, the presence of motility does not guarantee fertility, but the complete absence of motility is a very good indication that fertilizing capacity has been lost. There are various minor differences in the techniques which are used in different laboratories, but the one which we will describe is fairly typical.

Prior to the widespread dilution of semen for artificial insemination, motility referred almost exclusively to the degree of movement of spermatozoa in whole semen. It is now necessary to distinguish between the motility of whole and diluted samples. There is little similarity between the appearance of fresh whole semen and the same sample immediately after dilution. The appearance of good-quality fresh semen from the bull, ram, or cock, species with high sperm concentration, is that of millions of sperm in vigorous motion, and the semen itself has the effect of a body of water with fierce eddies and currents and a constant undulating movement. It is difficult to distinguish the behavior of individual cells in such samples, and even dead sperm appear to move because of the motion set up by the live sperm. Because of the dilution practiced in artificial insemination, there is little movement of the liquid itself, and individual sperm stand out clearly. It has been our experience in the conduct of artificial-insemination schools that if fresh whole semen is first used for demonstration purposes it is subsequently difficult to convince the trainees that diluted samples have any motility at all, to say nothing of the differences between good and poor samples.

The initial motility of fresh semen should be determined as soon as possible after collection of the semen. This should be done before the semen temperature has dropped much below body temperature. It is accomplished by placing a small drop of semen on a hanging drop slide in a warm room, or temperature can be maintained by the use of a special slide warmer. Various types of motility have been described, but the clinician usually distinguishes *rapid*, *progressive*, and *in place*, or *undulatory*, motility and scores semen samples on a basis of 0 to 5 in which:

5 = 80–100% progressive motility, swirling motion of the drop as a whole;

4 = 60–80% progressive motility, swirling motion indefinite or absent;

3 = 40–60% progressive motility, movement limited to individual spermatozoa;

2 = 20–40% of spermatozoa showing undulatory movement;

1 = 1–20% of spermatozoa exhibiting undulatory movement;

0 = no motility.

Semen which has been diluted with egg-yolk buffer is somewhat hard to see through under the microscope and the presence of large numbers of varying-sized yolk globules is confusing to the beginner. The standard for fresh semen which is described above is the one in general use with the exception that there is no swirling motion of the semen itself. The type of motility of the individual sperm is important. Samples which score 4 or 5 should contain sperm showing definite progressive motility, and the movement of the sperm should be sufficiently vigorous to agitate the yolk globules.

There are several factors which commonly affect motility and which will lead to incorrect estimates if not guarded against. There is a progressive decline in motility as temperature falls. The sample should be warmed, preferably to a standard of 80 to 90°F., if uniform results are to be obtained. The determination should be completed rapidly. Semen dries quickly in a warm room, and exposure to air inactivates the sperm. If an estimate is not made within a few seconds, a second sample should be taken. Dirty slides or traces of water or alcohol will affect the degree of motility. Although it cannot be said with certainty that a diluted sample scoring 1 will never produce fertilization, it can be said that the degree of fertility will be highest when samples scoring 4 or 4 plus can be used.

Duration of Sperm Motility.—It has been known for many years that there is a high correlation between the maintenance of sperm motility and the fertilizing capacity of sperm when either whole or diluted bull semen is stored at 5°C. If the samples are properly handled, motility persists for 2 weeks or more if the bull is of normal fertility. While this method is one of the better ones for the measurement of semen quality, it has the disadvantage of requiring a relatively great length of time and the evaluation is not completed until the original semen sample has long since ceased to be usable.

Weisman (1941) developed standards for the survival of human sperm stored at different temperatures. He reported that the survival times of normal human sperm at 20 to 23°C., 37.5°C., and 45°C. should be at least 24, 10 to 12, and 1 to 2 hours, respectively. Studies at Cornell by Beck and Salisbury (1943) showed that there were significant correlations between the decrease in motility of sperm in diluted bull semen stored at 5°C. and similar samples stored at from 46.5 to 47.5°C. The correlation coefficient of storage for 10 days at 5°C. and storage at 46.5°C. for 1 hour was 0.9088, indicating that by increasing storage temperature much valuable information in regard to the maintenance of motility can be gained in a short time. This method has many laboratory applications but is not widely used in the field.

The Methylene-blue Reduction Test.—The dye methylene blue loses its deep blue color when two atoms of hydrogen are added. This phenomenon of methylene-blue reduction has been used for many years as a technique in the measurement of certain types of cellular metabolism, especially in bacteria.

A method has been developed at Cornell for the evaluation of semen quality by determining the time required for semen of varying qualities to reduce a standard amount of methylene blue. Two-tenths ml. of bull semen is diluted with 0.8 ml. of yolk-citrate diluent in a small test tube. To this is added 0.1 ml. of a methylene-blue solution composed of 50 mg. of methylene blue dissolved in 100 ml. of sodium citrate buffer. When the tubes are incubated in a water bath at 45°C., the best samples reduce the blue color in 3.5 to 6 minutes. Poor samples require longer, up to 40 minutes (Beck and Salisbury). It was shown that there were high correlations between concentration of spermatozoa, sperm motility, and the amount of ascorbic acid in the semen and the time required to reduce the blue color. This method has been used in numerous bull studs as a measure of semen quality. Semen which requires more than 9 minutes to lose the blue color is regarded as subnormal.

This technique has been adapted to the semen of other species, but it is the writers' opinion that it seems to be better adapted for bull semen than for boar or chicken semen.

Measurement of Sperm Metabolism.—As indicated in the chapter on the male, the chemical nature of semen and the metabolism of spermatozoa have been favorite subjects for laboratory investigation. The glycolysis of semen and the oxygen consumption and carbon dioxide production of sperm can be measured. In a very general way there is a relationship between sperm numbers, motility and survival, and the type and degree of metabolism. However, these techniques are not easily adaptable to field conditions.

Differentiation of Live and Dead Spermatozoa.—The relative numbers of live and dead spermatozoa can be estimated by the direct microscopic examination of fresh semen. This method is obviously subject to considerable human error. Workers at the University of Missouri have reported a staining method for the differentiation of live and dead spermatozoa. The technique was first worked out for ram sperm by Lasley *et al.* (1942) and was subsequently modified for other species by Mayer *et al.* (1947). A stain containing fast green FCF and either eosin B or erythrocin B is made up in a phosphate buffer at a pH of 7.25, and a small sample of semen is stained according to very specific directions. Dead sperm are stained by such a mixture and live sperm remain unstained. This procedure appears to have been very reliable in the

hands of its originators, but others have obtained variable results. The method has been shown to be affected by minor changes in pH, osmotic pressure, and stain concentration, and the technique must be very carefully carried out (Mayer, 1948).

This method, or modifications of it, will have practical application if it can be controlled.

Number of Abnormal Spermatozoa.—Although Ham and Leeuwenhoek observed the spermatozoa of the human as early as 1677, it is only during the twentieth century that detailed studies of spermatozoa have been made. Williams and Savage (1927) made extensive studies of the morphology of bull spermatozoa and reported that in bulls with poor breeding records an average of 50.1 per cent of the spermatozoa were abnormal and that bulls with good breeding records averaged less than 16.6 per cent abnormal spermatozoa. These findings have been confirmed by Moench and Holt (1931), who found that men producing more than 25 per cent abnormal spermatozoa were of lowered fertility or sterile, and by McKenzie and Phillips (1934), who reported that normal rams produced not more than 15 per cent abnormal spermatozoa. Several slides of each semen sample to be examined should be prepared at the time of collection. This can be accomplished by placing a very small drop of thoroughly mixed semen at one end of a glass slide and drawing it out in a *very thin* film in the same way that blood smears are made. Considerable practice is required to make satisfactory slides of highly concentrated semen. The problem is one of obtaining a smear thin enough for study without mechanical damage to the spermatozoa. The slides may be allowed to air-dry and then may be placed in a saturated chlorazene solution for 5 to 10 minutes to remove mucus. They should then be rinsed in distilled water, washed in 95 per cent alcohol, allowed to dry, then stained with Ziehl's carbol-fuchsin for 1 to 2 minutes, rinsed in tap water, and allowed to dry. The stained slides should be studied under high-dry or oil-immersion objectives and classified by some definite scheme.

Nearly as many systems of classification as there have been investigators have been devised, but the abnormal sperm types most usually encountered are head abnormalities such as tapering, shrunken, large, or small heads; enlarged, beaded, broken, or filiform middle pieces; and coiled, broken, or missing tails. A study of a single smear of semen is sometimes misleading, for seasonal effects, excessive use, or long periods of sexual rest are among the factors that may temporarily increase the number of abnormal spermatozoa. McKenzie and Berliner (1937) in an extensive study of the reproductive capacity of rams found that, under Missouri conditions, the number of abnormal sperm forms increased

during June, July, and August and were at a minimum during November, December, and January. Shropshire rams were more noticeably affected than Hampshire rams, the former having an average of 733 and the latter an average of 90 abnormal sperms per 1,000 during August.

Semen samples collected after prolonged periods of sexual rest should not be used for the determination of fertility. Spermatozoa that are not ejaculated tend to become senescent and are eventually broken down and resorbed. This fact often accounts for the failure of males to settle the first females to which they are bred at the beginning of the breeding season and must be taken into account in the estimation of fertility.

A few years ago this measurement was considered essential in the evaluation of semen. More recently the emphasis has been on the physiological measurement of semen quality. The determination of abnormal sperm forms will frequently distinguish between superior, questionable, and inferior semen samples, but it has never been possible to predict relative fertility very closely.

pH of the Semen.—The development of the glass electrode pH meter, as well as a variety of special test papers for different pH ranges, makes possible the accurate measurement of hydrogen-ion concentration of semen. Unfortunately, this measurement is of little value in practical semen evaluation since the pH range of semen does not ordinarily fluctuate widely.

Purity of Semen.—Semen should be collected and maintained as free of microorganisms, cellular debris, dirt, blood cells, urine, or other foreign matter as is humanly possible. There would be no quicker way to spread genital diseases than by the use of semen containing such organisms. Many substances such as red- or white-blood cells, urine, water, soap, disinfectants, or secretions of the female genitalia are either toxic to spermatozoa or adversely affect their viability and should not contaminate semen.

PROCESSING AND SHIPMENT OF SEMEN

Cooling Semen.—Many substances should be cooled as rapidly as possible to prevent degenerative changes, *e.g.*, milk, meat, and foodstuffs which are to be preserved by quick freezing. Semen should be cooled to about 4 or 5°C. (40°F.) in order to maintain sperm motility for maximum periods of time, but it is now known that too rapid cooling will permanently reduce sperm viability. This is called temperature shock, and it has been reported in several species.

Temperature shock must be prevented, especially during the collection of semen and before the semen has been diluted. The glass receptacle on the artificial vagina which is to receive the semen should be warmed

before use and protected by insulation during the winter months. An artificial vagina in which the receptacle is surrounded by the water jacket was developed at Cornell and has proved practical.

Immediately after collection, semen should be taken into a warm, dust-free room and motility score and sperm numbers determined. If the sample is clearly of good quality, it is usually diluted at once with fresh dilutor which has been warmed to about 80°F. It is important that the semen and dilutor be approximately the same temperature, and since fresh collected semen cools to about 80°F. rather quickly, this temperature is a practical one.

The diluted semen should then be cooled at the rate of about 1°F. per minute until the storage temperature of 40°F. has been reached. This can be accomplished in the laboratory by electrically operated devices, but under practical conditions it is usually done by placing the semen container in several changes of water, each a little cooler than the preceding one.

By a little practical experimentation the semen container can be put in a jar containing water at 80°F. and then placed in a refrigerator. By adjusting the respective volumes of semen and water, the semen can be made to cool at the required rate.

Semen Diluters.—Many substances have been used for the dilution of semen, but most of them have been lacking in one or more of the qualities of a practical diluter. In order to be suitable for use in practical artificial insemination a diluter must maintain the fertilizing capacity of the sperm for maximum periods of time, it must be easily prepared, of readily available substances, be low in cost, and nonirritating to the recipient of the semen. The history of the diluter problem is a long one and has not been confined to the bovine species. Among the materials tried have been physiologic saline solution to which has been added numerous organic and inorganic substances including glucose, amino acids, vitamins, hormones, drugs, and antibiotics. Nearly all the body fluids and secretions have been tried, blood plasma, blood serum, spinal fluid, milk, reproductive accessory-gland secretions, and semen plasma itself.

In 1940 Phillips and Lardy developed a diluter made up of egg yolk and phosphate buffer for cattle semen. This diluter was widely adopted and is still in general use. The phosphate buffer contains 0.2 g. of KH_2PO_4 and 2.0 g. of $NaHPO_4.12H_2O$ in 100 ml. of sterile redistilled water. To facilitate its preparation, capsules containing the proper amount of chemicals for addition to the water are commercially available. Fresh egg yolk is prepared by the complete separation of the yolk from the albumen, puncturing the membrane surrounding the yolk, and allow-

ing it to run into a clean sterile graduate. Equal parts of phosphate buffer are mixed with the egg yolk and the yolk buffer is ready for use in semen dilution.

At this point it should be emphasized that only chemically pure ingredients should be used, that water redistilled in a glass still is required, that fresh eggs from hens fed a balanced ration should be used, and that substances or conditions which might be toxic to sperm must be avoided.

A second practical diluter was developed by Salisbury *et al.* at Cornell in 1941. It was made up with egg yolk and a sodium citrate buffer and has since been modified by Salisbury and Bratton (1948) to contain sulfanilamide. The citrate buffer is made up of 3.6 g. of sodium citrate dihydrate ($Na_3C_6H_5O_7.2H_2O$) per 100 ml. of glass distilled water and the buffer is then autoclaved for 20 minutes at 15-lb. pressure. Equal parts of buffer and fresh egg yolk are mixed. Sulfanilamide is added at the rate of 300 mg. per 100 ml. of diluter.

Several entirely satisfactory diluters are readily available for cattle semen, the yolk-phosphate diluter, the yolk-citrate diluter with or without sulfanilamide, a commercial synthetic pabulum, and a commercial, completely prepared, modified egg yolk-citrate diluter ready for immediate use.

There has been relatively little use of diluters for ram, boar, and chicken semen in the United States. Numerous diluters have been used in Europe and Asia, and their composition has been discussed by Anderson (1945).

Several diluters suitable for stallion and jack semen have been described by Berliner (1945). These contain egg yolk, glucose, and K-Na tartrate and gelatin in varying amounts, depending on the exact purpose for which the diluter is to be used.

Dilution Rate.—Theoretically, only one sperm is necessary for the fertilization of an ovum and only one specific microorganism for the establishment of a disease. In practice, however, it is unlikely that only one cell will produce such results. This has been explained in numerous ways, the most plausible of which may be that large numbers are necessary, since many of the cells are lost on the way to their destination.

Many of the earlier estimates of the number of sperm required for fertilization have been nullified because of advances in knowledge and techniques in semen physiology. In rabbits, for example, in 1927 it was thought that 1 million sperm were necessary for maximum fertility and that sterility was reached if there were 100,000 or fewer sperm. In 1946 it was concluded that maximum fertility could be attained with 330,000 to 420,000 sperm and minimum fertility with 40,000. In 1948 it appears

that 16,000 sperm will give partial and 90,000 spermatozoa maximum fertility (Cheng and Casida, 1948).

The first work in artificial insemination involved the use of fresh undiluted semen. In practical cattle insemination semen was diluted three to four times in 1940 and about 1:10 to 1:16 in 1945. Salisbury (1948) reported that there were no differences in fertility when bull semen was diluted with egg yolk-citrate diluter at a rate of 1:100 in comparison with rates as low as 1:40. One ml. of diluted semen containing about 12.8 million sperm was used for each insemination. It has since been reported that there were no differences in conception rate when yolk-citrate-sulfanilamide diluter was used at rates of up to 1:400. It was pointed out that with present techniques the minimum number of sperm for optimum fertility is between 5 and 10 million if bulls of known fertility are used (Salisbury and Bratton, 1948).

Much work on dilution rate and composition of diluters is in progress, and it should be recognized that these results may need further modification. As previously explained, the diluter problem is of less practical importance in the other classes of farm animals, and data similar to those given for cattle are not available.

Storage and Shipment of Semen.—In artificial-insemination practice semen is rarely stored at its point of origin but by the local inseminator. The chief problem is one of the maintenance of optimum conditions during shipment and while the semen is being transported by the inseminator on his rounds.

The type of shipping container depends on the volume of semen which is to be sent and the distance involved.

When single semen samples are to be shipped, as is usually the case when semen from a particular sire is purchased by a breeder at a distance, an ordinary thermos bottle can be used. It is desirable that the temperature of the semen be maintained at a uniform 4 to 5°C. during shipment. This can be accomplished by placing a full tube of semen within a second larger container, taking care to separate the two with cotton. Both containers should be watertight. The larger container is then surrounded by cracked ice, the thermos bottle placed in a sturdy cardboard carton and shipped.

When the time of shipment is 2 or 3 days, the thermos bottle itself should be packed in a refrigerated container. A small, jacketed, insulated ice-cream shipper has been successfully employed at the University of Missouri. The thermos bottle is placed in a metal can and surrounded by cracked ice and a can or block of frozen brine is placed on top of the can containing the cracked ice (Herman and Ragsdale, 1946).

In most states semen can be shipped from the bull stud to all local associations within 12 hours. The equipment required for this is surprisingly simple.

The refrigerant is provided by one or two milk cans approximately 2.5 by 4 in. The cans are filled to within about an inch of the top with water, sealed, and frozen solid. Two layers of heavy wrapping paper are placed about the cans, and the semen vials are then placed against the wrapped cans and firmly wrapped with several layers of paper. This package is placed within one insulated paper ice-cream bag during the cooler months and within two insulated bags during the summer. This in turn is placed in a heavy corrugated cardboard box and shipped by common carrier. This equipment is light in weight, inexpensive, and readily available commercially.

The vials containing semen should be as nearly full as possible. If only a small quantity of semen is to be sent, a small vial should be used. It is known that the mixing of semen with air by agitation during shipment is undesirable and results in decreased sperm motility (Prince and Almquist, 1948).

The experienced inseminator can usually tell if semen shipments are arriving at the proper temperature. If the ice in the cans has melted, it is well to check the temperature of the semen with a thermometer and report abnormalities to the bull stud.

All semen samples which the inseminator plans to use should be examined microscropically each day. There are times when a 48-hour-old sample may be superior to a fresh one. Knowledge of the actual fertility of the bulls and experience in semen evaluation will soon enable the inseminator to select the samples most likely to produce pregnancy. The inseminator usually receives fresh semen six or seven times weekly. It is obvious that he cannot guarantee that the semen of a particular bull will be used to inseminate a particular cow. However, by adhering to recommended practices, he usually has the semen of several bulls of each breed available, even though the semen is of different ages.

In the past there has been much wishful thinking in regard to the storage possibilities of semen. With rare exceptions bull semen should be used within 2 to 4 days following collection if good results are to be expected. Ram semen should be used within 2 days; and boar, stallion, and chicken semen should be used on the day of collection. To the authors' knowledge the maximum survival of sperm for conception is 10 days, 6 days, 56 hours, and 48 hours for bulls, ram, boars, and stallions, respectively. These results have been obtained with stored semen and represent maximum rather than average values.

The maintenance of maximum fertility in stored semen requires special

handling by the inseminator. The semen should be maintained at a uniform 4 to 5°C. while in his care. It is recommended that inseminators be equipped with portable refrigerators of the type commonly used by veterinarians. The semen vials are transported in small thermos bottles, and the thermos bottles in turn are kept in the portable refrigerator. Care should be exercised that the semen is not allowed to remain out of the refrigerator except for the time required to fill the inseminating pipette.

TECHNIQUE OF INSEMINATION

The method of insemination will depend both on the species and the experience of the operator. The methods commonly used for cattle will be described in detail and but briefly for the other farm animals.

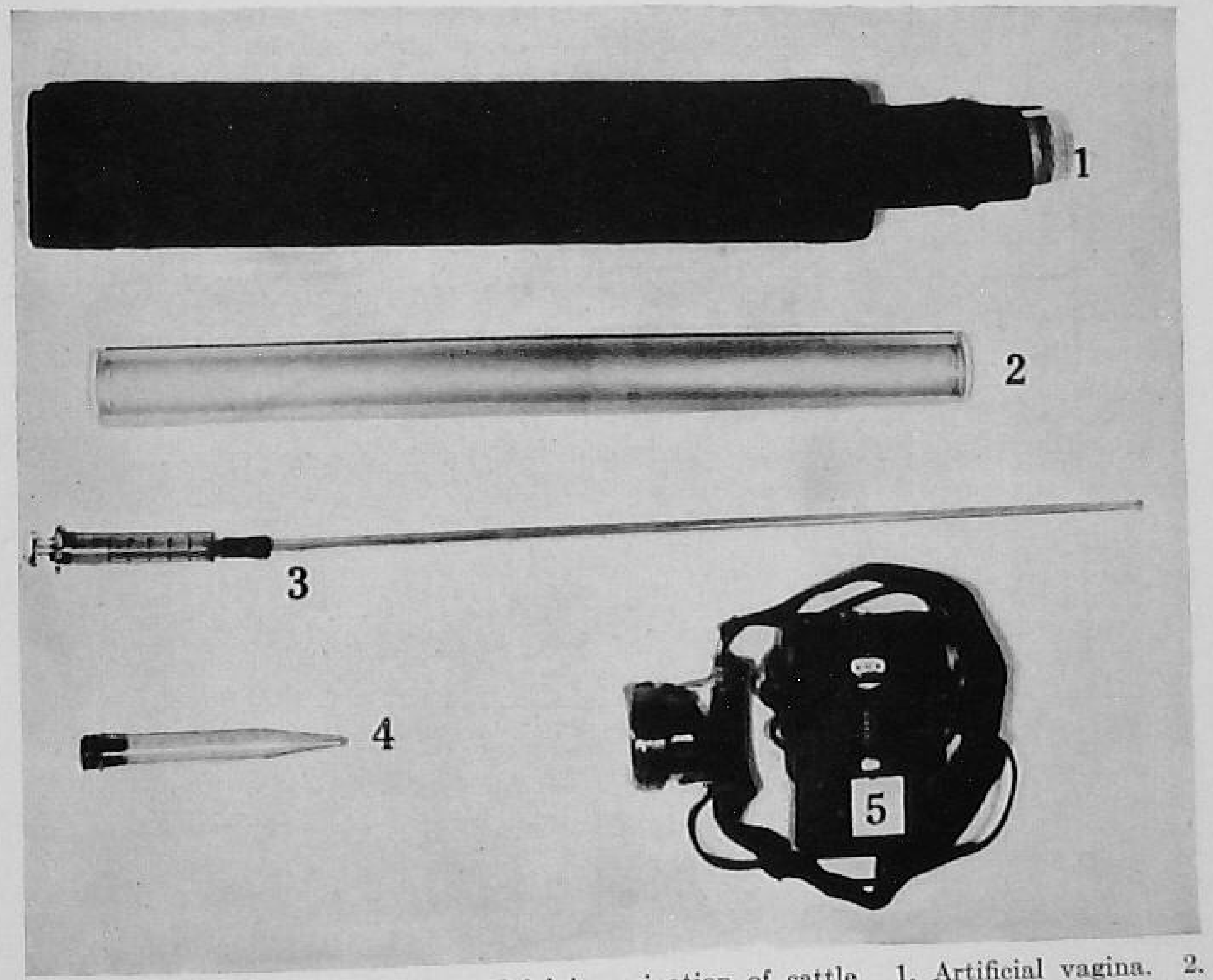

FIG. 80.—Equipment for the artificial insemination of cattle. 1. Artificial vagina. 2. Lucite or glass speculum. 3. Inseminating tube and syringe. 4. Graduated test tube. 5. Head lamp.

If economy of semen is no object, the deposition of several milliliters of whole or diluted semen in the vagina of the cow will give satisfactory results. Since the chief advantage of artificial insemination is to extend the usefulness of superior sires, this method has little merit. The method in common use prior to 1940 involved the partial penetration of the

cervix with an inseminating tube while it was visualized through a vaginal speculum. This technique seemed to have the advantage that the operator could *see* what he was doing, but we now recommend that he *feel* what he is doing. The muscular tensions which are set up following the introduction of the speculum make it difficult if not impossible to penetrate the cervix further than the outer region. Under practical conditions it is probable that the semen is frequently not deposited in the cervix at all. It has the disadvantage of requiring a large supply of sterile specula, one for each cow, and the chore of cleaning them can be a laborious one. The method does give satisfactory results and is still used.

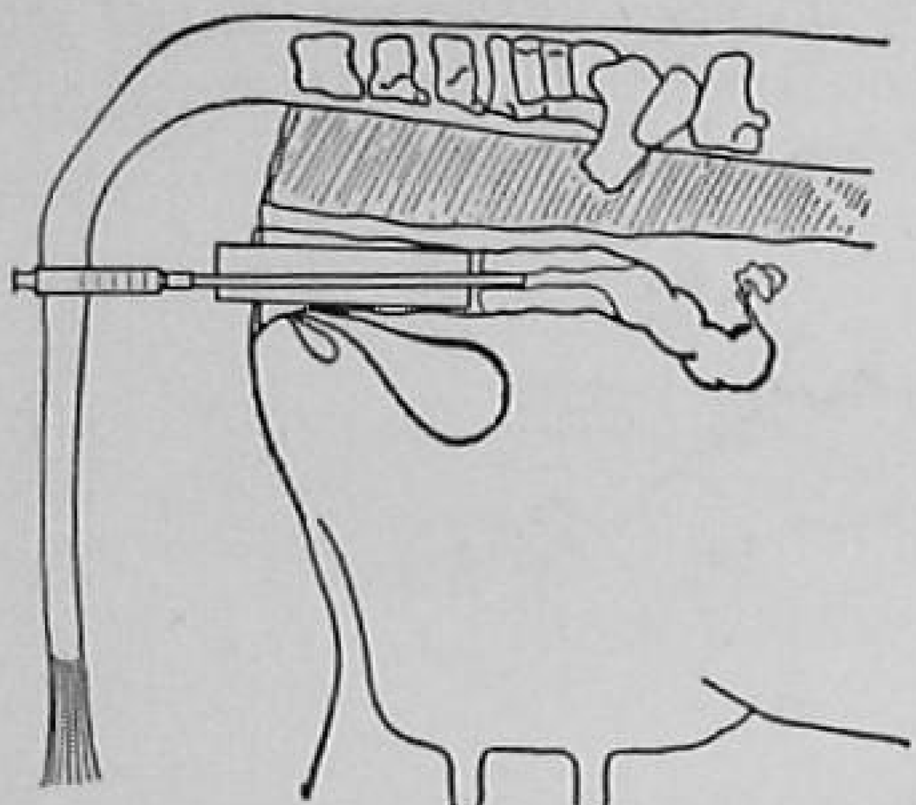

FIG. 81.—Insemination of the cow involving the use of a vaginal speculum. The cervix is visualized and the inseminating tube is passed into the first part of the cervical canal.

The technique in most general use at present is the grasping of the cervix with the left hand in the rectum and the introduction of the inseminating tube through the vagina and into the cervix with the right hand. By the rectal manipulation of the cervix, the tube can be guided through the cervix and even into the uterine horns. This method is rapid, requires a minimum amount of equipment, and is less likely than the speculum to introduce foreign substances into the vagina.

The step-by-step routine recommended for inseminators is as follows: (1) Don clean work clothing, boots, and rubber sleeve as soon as arriving on farm, (2) positively identify cow, (3) locate equipment case and pail of warm water near cow, (4) attach clean inseminating tube to syringe and fill with 1 ml. of desired semen, (5) place inseminating equipment on special hooks on lid of case, (6) lubricate left hand and arm with soap or other lubricant, (7) enter rectum carefully and remove feces, (8) wipe manure from rear quarters with fresh paper towels or cotton, (9) wipe lips of vulva with small quantity of fresh cotton, (10) grasp cervix firmly, (11) insert inseminating tube into vagina and approach cervix carefully, (12) introduce tube into cervical opening, (13) work cervix back and forth and up and down, working tube into body of uterus, (14) deposit semen.

The inseminator must have a basic knowledge of bovine anatomy and physiology and above all must exercise good judgment. Carelessness may result in perforation of the vaginal wall or injury of the cervix or uterus. Inseminators are frequently called to service cows which are

already pregnant. The penetration of the cervix of a pregnant animal is almost certain to result in abortion. It may be impossible to prevent such occurrences in the first few weeks of pregnancy. If the cervix is tightly closed and dry, little is gained by trying to force penetration. The cow may not be in heat or she may be pregnant.

A very routine inspection of the cow may reveal an anatomical defect of the genitalia, inflammation, or infection. Artificial inseminators are

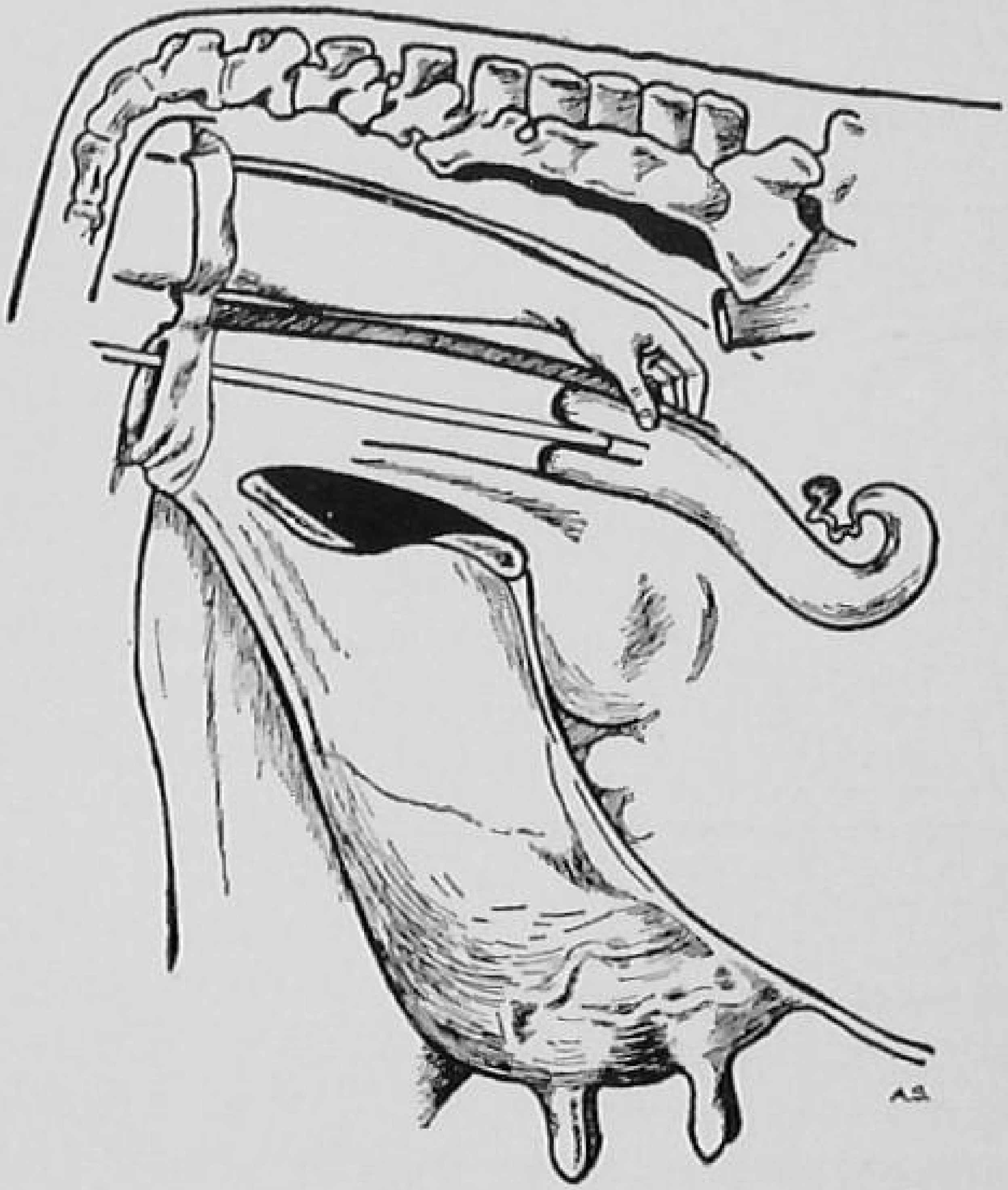

FIG. 82.—The most common technique of inseminating the cow. The cervix is grasped *per rectum*, and the inseminating tube is carefully worked into and through the cervical canal.

neither trained nor expected to diagnose reproductive disturbances. When it is obvious that some type of an abnormality is present, it should be called to the attention of the owner in order that he may secure veterinary assistance.

The mare is the easiest of the farm animals to inseminate. Mares should be hobbled in order that the inseminator may work in safety. The tail of the female should be wrapped with a clean bandage of the type used on the legs of running horses. The region around the vulva can be cleaned with a damp sponge and the lips of the vulva wiped with a piece of clean cotton. The operator should wear clean, dry rubber gloves which have been previously washed in alcohol or some similar

disinfectant. Fresh semen is poured into ½-oz. gelatin capsules and quickly inserted as far forward in the cervix as possible. Twenty ml. of semen per insemination is sufficient in small mares and 30 to 40 ml. in large multiparous females. The semen can also be introduced through the cervix with a catheter attached to a syringe or a flask equipped with a pressure bulb. As previously mentioned, mares should be inseminated more than once during estrus if maximum fertility is to be attained.

Sows are usually inseminated with a rubber catheter attached to a syringe. The cervix can be penetrated by a fairly stiff catheter and the semen slowly deposited in the uterus. If the cervix is not entered, much of the semen will be lost from the vagina. There is relatively little known about the volume of semen and numbers of sperm required for swine. Under practical conditions 20 to 50 ml. of whole semen can be expected to give satisfactory results. There is evidence that much smaller quantities of semen, when properly diluted, may be satisfactory, but this has not been verified under herd conditions.

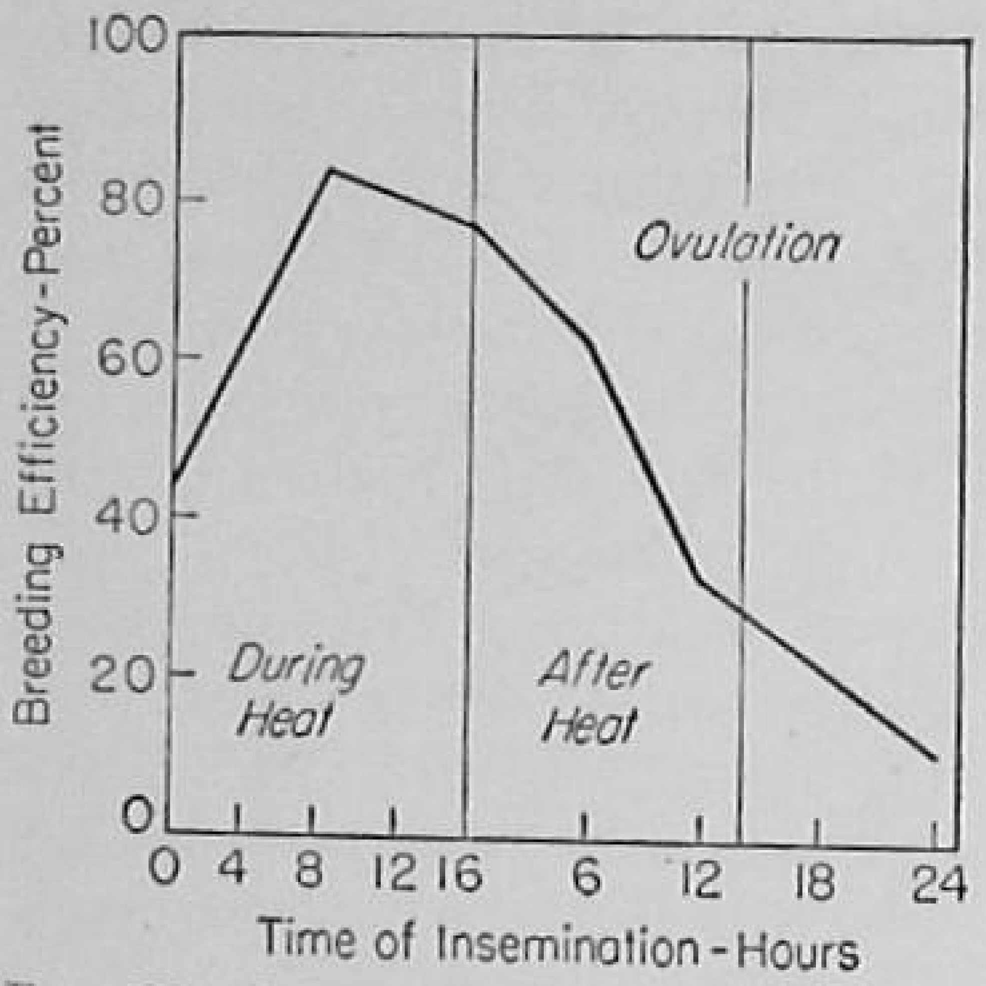

FIG. 83.—Relationship between time of insemination and breeding efficiency in dairy cattle. (*Adapted from the data of Trimberger and Davis* (1943), *Neb. Agr. Expt. Sta. Res. Bul.* 129.)

Ewes are usually inseminated with the same type of pipette or tube that is used for cattle. The pipette is filled and emptied with a syringe or small rubber bulb. The cervix is visualized with a speculum and a small flashlight or headlamp and the pipette introduced into the outer part of the cervix—probably not more than ¼ to ½ in. A volume of 0.2 ml. is usually used both for whole or diluted semen. The egg-yolk diluters used for cattle have been successfully employed for sheep. There is considerable difference of opinion in regard to sperm numbers required, ranging from 5 to 50 million.

Artificial insemination has not been widely employed in poultry. It is very useful when hens are being maintained in individual laying cages, as in many nutrition and breeding experiments, and it has a place on certain practical poultry-breeding farms. Hens are usually inseminated with fresh semen once weekly. The oviduct of the laying hen can be easily protruded by applying pressure in the cloacal region. A 1-ml. tuberculin syringe, without a needle, is inserted into the oviduct

to a depth of about 1 in. and 0.1 ml. of semen deposited. A single weekly insemination can be expected to yield about 90 per cent fertility. A limited amount of work with diluters has been done, but thus far most inseminations are made with fresh whole semen.

Organization of Artificial Insemination.—The advances in artificial-insemination techniques which have occurred during the last decade have resulted in a complete revision of our ideas with respect to the organization and operation of artificial-breeding associations. Since nearly every state has extension specialists who concern themselves almost exclusively with artificial insemination, we recommend that such specialists be consulted in regard to local conditions.

In a very general way artificial insemination is being used by three groups in the United States, the purebred breeder, the local association, and the central breeding unit. The purebred breeder has long employed artificial insemination on a more or less private basis. It has been used to extend the services of valuable sires within and between herds and for the control of certain genital diseases. The fees for such services depend upon the relative value and popularity of the sires, and there is a growing demand for this type of service.

A few years ago we thought that the local artificial-breeding association was most likely to be successful. Organizations of this type may be cooperatively or privately owned and usually serve an area with a radius of about 20 mi. Many such associations were established between 1938 and 1942. Some have been completely disbanded, some have become a part of a larger organization, and some are still in successful operation. The chief reasons for modification have been economic. The difficulty and cost of obtaining suitable bulls has been a major problem. The number of bulls necessary to serve 1,200 cows of three different breeds, and still provide a safety factor in case some of the bulls become sterile, is nearly as great as is needed to serve 10,000 cows or more. In short, the cost of semen per cow served in a small local organization is greater than when many local associations are served by a central bull stud.

The general trend in artificial insemination is toward the central breeding unit. In this type of organization the bulls are maintained in a centrally located stud. Well-equipped laboratories and technicians specially trained in the care of bulls and the processing and shipping of semen are a definite requirement for the success of this type of unit. Semen production is thus concentrated in one place, and the actual insemination of the cows is carried out by local organizations. The problem of locating new sires is of sufficient importance to require permanent personnel specially trained in selection. The need of keeping abreast of the latest developments in semen physiology is essential.

It appears that these problems can best be met when some of the workers devote themselves exclusively to bull-stud work, and others to the insemination of cows.

In some of the larger states there are several bull studs located in strategic areas, each serving numerous local insemination associations. The type of organization in Indiana is described briefly not only because of the authors' familiarity with it but because of certain unique features. Local artificial-breeding cooperatives obtain semen from bull studs in both Indiana and North Carolina. On alternate days semen from the North Carolina stud is transported by airplane to the Indiana stud and thence to local associations. And every other day semen from Indiana is shipped to North Carolina where it is distributed to local associations in North Carolina, Georgia, Florida and Virgina. From the economic standpoint semen which is produced but not used represents waste, and it has long been apparent that we have not been getting the maximum use from our sires. The safety factor cannot be overlooked, however, and it is regarded as essential that there be some reserve of semen production. The regular exchange of semen between states does make for a wider use of outstanding sires, and it offers some protection to the livestock owners of both states in case of serious trouble at one of the bull studs, such as fire or disease.

Artificial Insemination Problems.—It is obvious that artificial insemination is established as a practical method of livestock breeding but it is equally obvious that its applications and techniques are being constantly changed and improved.

The method of processing and shipping bull semen can be regarded as satisfactory. That constant improvement is being made is evidenced by the fact that recommended dilution rates have increased from 1:10 to 1:100 within the past 5 years and that greater dilution is still possible. Only when it becomes possible to maintain the fertility of bull semen for weeks, instead of 3 or 4 days, or even after the sire which produced the seman is dead, will physiologists be satisfied with their progress.

The proving and selection of sires for artificial-insemination use is a major problem. A suggested method for proving sires at a young age has been proposed. The tendency for fertility level to decline in bulls more than two or three years of age, and the fact that many proved sires are not of suitable fertility, are limiting factors. We need more knowledge about the basic reproductive processes before these problems can be overcome.

The rapid adoption of artificial insemination has resulted in a shortage of trained technicians. In states where several artificial-breeding associations have been established simultaneously, there has usually been

an unsatisfactory conception rate during the first few months of operation. This is apparently due to the inexperience of both technicians and herd owners. There is no substitute for insemination experience and good livestock sense. Many owners had no idea that their animals had not previously conceived on the first natural service and were openly critical of artificial-insemination conception rates of 50 per cent. Some owners knowingly submitted shy breeders for insemination in the expectation that it would overcome the difficulties. Others do not yet understand even the elementary principles of reproduction and have not appreciated the necessity of keeping breeding records and studying the estrual behavior of their cows. These problems are being overcome by the improvement of courses for training inseminators and providing them with an opportunity to serve an apprenticeship with an experienced inseminator. Efforts to increase the knowledge and interest of owners in breeding management are bearing fruit.

One of the major unsolved problems is that of infertility. This is not peculiar to artificial insemination but concerns the whole livestock industry. As discussed in another chapter, the failure of animals to conceive promptly and produce strong healthy young is of great economic importance. This is not one disease or condition but a complex including the whole field of biology. Only by much basic research will the solutions be obtained.

The production of physically and genetically superior offspring is of no value unless the environment is suitable for the expression of each animal's capabilities. Cows genetically capable of producing 400 lb. of butterfat will not do so if managed in the same way as their 200-lb. dams. One of the most encouraging results of artificial insemination has been the development of new interests of livestock owners in better management, but these interests need much further development.

Transplantation of Fertilized Ova.—The outstanding success of the transfer of sperm to the female genitalia by instruments rather than by natural service has led to speculation in regard to the transfer of ova from one female to another. This idea, although not so old as artificial insemination, was rather well developed in the latter part of the nineteenth century. Between 1880 and 1897, European and British biologists succeeded not only in the recovery of rabbit and guinea-pig ova but in their fertilization outside the body and in the transfer of fertilized ova from one female rabbit to another.

As described in the chapter on the female, the techniques for the fertilization of rabbit ova outside the body and their subsequent transfer to other females where normal embryonic development occurs have been highly developed. In addition, Pincus has reported the development of

the rabbit ovum without stimulation by sperm. As also mentioned, techniques for superovulation, the production of large numbers of ova, were described for rats and mice over 20 years ago and have more recently been developed for cattle and sheep at the University of Wisconsin.

The groundwork has thus been laid for the transfer of fertilized ova from genetically superior females to ordinary healthy females which would carry on embryonic and fetal development. In this way, superior females

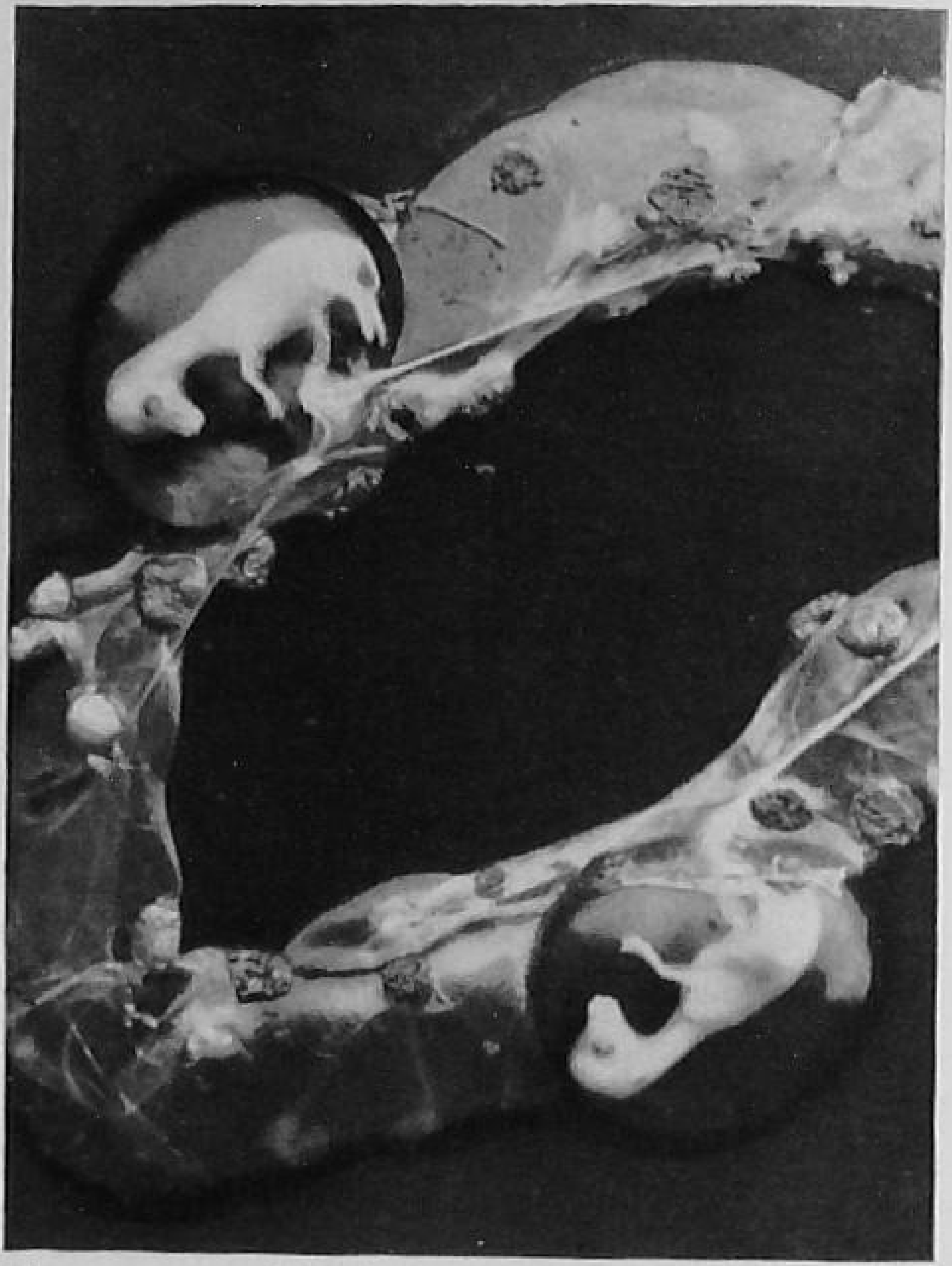

FIG. 84.—Twin fetuses recovered 46 days after the transfer of fertilized sheep ova to a second ewe. (*Courtesy of Drs. Casida, Warwick, and Murphree, University of Wisconsin, February, 1942.*)

would be spared the burden of pregnancy and would be free to produce ova at regular intervals. That this can be done in the laboratory has been established for nearly 75 years; whether it can be done repeatedly with the same animals on a practical basis remains to be seen.

Several problems are immediately apparent, and there are undoubtedly others which are not yet known. One of these involves the number of ova. Should the ovaries be allowed to produce at a normal rate and the ova be collected at each heat period? If surgical procedures are

necessary, the risk involved for the recovery of one or two ova per operation may be excessive. Operative losses, as well as effects on the future production of ova, must be considered. The production of great numbers of ova at one time (30 to 40) by superovulation techniques has the advantage of balancing the risks with the possibilities of securing more ova than would ordinarily be produced in the lifetime of a cow. Two other problems immediately arise. How frequently can superovulation be produced in the same animal and will future ovarian function be interfered with? Are superovulated ova capable of normal embryonic and fetal development? These questions cannot yet be answered in cattle. In some species the gonads become refractory to repeated treatment with gonadotropic hormones. The work available thus far indicates that there is a very high mortality rate in superovulated fertilized ova (Casida *et al.* 1943–1944).

The transfer of recovered fertilized ova to other females may be relatively simple, once sufficient basic information is available, or it may be very complex. It is possible that the ova may be transferred using the same techniques that are employed for artificial insemination, or it may be necessary to place them directly in the Fallopian tubes. In either case, it should be possible of accomplishment. The endometrium of the uterus undergoes almost constant change throughout the estrual cycle. The preparation of the uterus for implantation and the development of the fetal and placental membranes require a high degree of coordination between the endocrine glands, the uterus, and the zygote. It would seem desirable that the recipient female be in almost the same stage of the estrual cycle as the donor. This would require the maintenance of a large number of prospective recipient females. It might be possible to overcome some of these timing problems by the regulation of the time of superovulation, by the storage of fertilized ova, and by the hormonal regulation of the cycles of the recipients.

Summary.—We have defined artificial insemination as the deposition of spermatozoa in the female genitalia by instruments rather than by natural service. We have tried to emphasize the fact that this method of breeding is the most valuable tool yet developed for extending the services of outstanding sires at a cost which even the smallest herd owner can afford. It is apparent that artificial insemination is here to stay and that there are no disadvantages which cannot be overcome if recommended practices are strictly adhered to. It is likewise apparent that, before artificial insemination can be better than it is, we must expect to do those things which we think at the present to be best but ready to adopt new practices when they are proved to be better.

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SECTION III

Mechanisms of Heredity

CHAPTER XI

HISTORY AND PROBLEMS OF GENETICS

Genetics is the science dealing with the similarities and differences exhibited by related organisms. The science of genetics is one of the most recent of man's accomplishments, for it came into being with the rediscovery of the Mendelian principles of inheritance in the year 1900. A long series of events, which might be thought of as extending back to the beginnings of agriculture and the artificial selection of breeding animals following their domestication, preceded its birth. There are, however, three very important and definite milestones that mark the progress of events leading up to genetics. The first was the promulgation of the cell theory by Schleiden and Schwann in the year 1838. Hooke had noticed and discussed the cellular structure of cork in 1665, and, though this in itself led to nothing of moment, it is the historical introduction of the cell theory. The work of Schleiden with plants and Schwann with animals indicated that all living forms were built up of smaller units called *cells*. The discovery of the physical make-up of living things was significant. It founded the science of cytology, which after a rather slow beginning has yielded abundant returns, especially since 1870. The next milestone was that of the establishment of the evolutionary theory.

As we saw in Chap. III, many men had theorized about an evolutionary process before Charles Darwin in the nineteenth century marshaled the evidence that made it seem the most plausible explanation of the presence of the manifold forms of life which have inhabited or do inhabit the planet Earth. Likewise, the work of many men since Darwin's time has added to the plausibility of the theory. This theory ties all living forms into one organic related whole, with the whole of organic life subject to the same basic physiological laws and principles of conception, birth, metabolism, reproduction, inheritance, and death. Evolution postulates that all forms of life have arisen from other preexisting forms back to the time when life had its origin from nonliving materials, and that the rise of new species has been due to variation and selection. Evolution, therefore, is racial "becoming," whereas genetics is individual "becom-

ing," the same general principles underlying both processes. The third milestone was Mendel's epochal work on the behavior of characteristics in transmission, concerning which the next several chapters will deal.

Content of Genetics.—Bateson in 1906 coined the term *genetics*, which from its derivation from the Greek root *gen*, to become, literally means the *beginning*, or *coming into being*, of organic life. Genetics, however, does not stop with parturition or birth, but rather it expresses the idea of the full becoming of the individuality of the organism. This point should be borne in mind constantly by the student. Broadly speaking, genetics is the study of the why and wherefore of individuality. It is obvious that the individual will be either like its parents or different from them. What genetics attempts to do is to systematize knowledge regarding these similarities and differences and to furnish a rational explanation for them.

There is an old deep-rooted belief to the effect that "like begets like." Experience teaches that sows bring forth pigs not calves, and in this sense "like begets like," but, when the attempt is made to apply the idea in minute details to parent and offspring, difficulties are encountered. Although there may be, and generally is, a greater or less degree of similarity between the two, the expectation that parent and offspring may be exactly alike causes many a disappointment. The fact of the continuity of the germ plasm would lead one to expect that offspring would resemble their parents to a greater or lesser degree, and this, in truth, is just what observation teaches. Any organism receives the determiners for all its potentialities from its ancestors through its immediate parents. It is inconceivable that they could come from any other source, and there is no evidence that any animal can exceed in its accomplishments the upper limit set by its inheritance.

The sum total of all the possibilities and accomplishments of an organism is its individuality. This may appear as the expression of characteristics exactly similar to those exhibited by any of its ancestors, a blend or a mosaic of ancestral characteristics, or one or many very different characteristics due to the interaction of ancestral genes or to mutation. Strictly speaking then, it may be seen that an organism's individuality is the sum total of all its characteristics which result from the union of germ cells produced by its particular parents plus the influence of the environment in which the individual develops. Genetics seeks the cause and the pattern of transmission of ancestral traits down through the generations, to find rational explanations for the occurrence of new traits, and to differentiate the relative influence of inheritance and environment.

Environment and Training.—Two organisms may have different genes but be similar in appearance or behavior because of the environment.

Likewise two organisms may have identical genes but be different because of the environment. We shall lay particular stress upon the complement of ancestral determiners, or upon an animal's inheritance. The student, however, must not forget that two other influences aid in shaping individuality, *viz.*, environment and training. Any individuality is a product of the interactions of these three influences and, although resting on the complement of ancestral determiners as its base, this does not in any way minimize the influence of the other two. Many variations are due to environmental causes. The complement of ancestral determiners, however, does set the upper limit that an organism can reach. It is a breeder's province, therefore, to select breeding animals that will set a high upper limit for their offspring and then so to modify environment and training that that limit may at least be approximated.

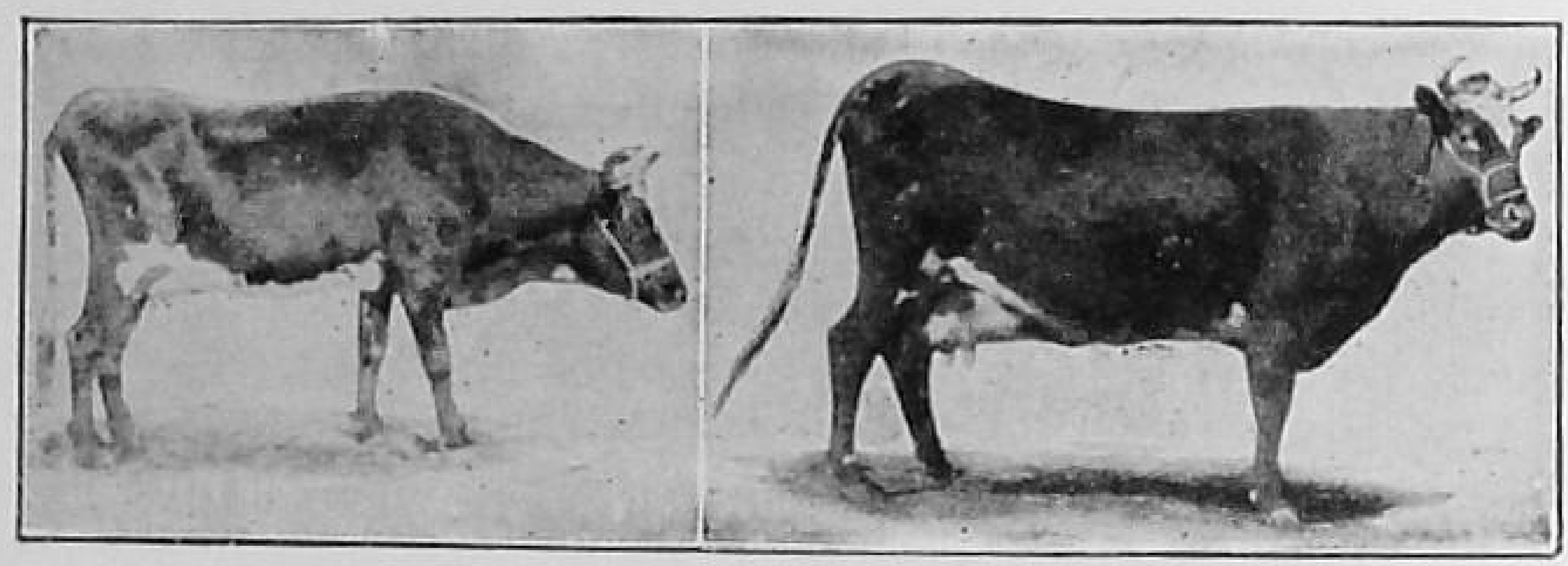

FIG. 85.—A scrub cow before and after being subjected to a good environment. Besides the increase in condition evidenced in the pictures, she increased in production 2,814.6 lb. of milk and 113.75 lb. of fat. (*From Iowa Expt. Sta. Bul.* 188.)

Pre-Mendelian Animal Breeding.—Man has been selecting plants and animals for an unknown period of time, perhaps 10,000, 25,000, or 50,000 years. His method has always been the very simple one of mating what he considered desirable animals and basing his hopes on the general principle that "like begets like." From an early date his selections were probably influenced to some extent by a consideration of pedigree and also to some extent by demonstrated ability to beget desirable offspring. Up until the very recent past, the mechanisms of reproduction, hereditary transmission, and variation were totally unknown. Just by trial and error man made wonderful progress in creating more beautiful and efficient animal types. The scientific basis of inheritance has unfolded rapidly since 1900, so that the modern breeder need no longer be handicapped by a lack of the knowledge of basic principles.

It is sometimes disparagingly remarked that man has made no progress in breeding better livestock for the past 100 years. Since the breeder is unable, up to the present at least, to create new genes for desirable

characters, such a statement is tantamount to saying that breeders have not discarded any undesirable genes or increased the number of desirable ones, or put them together into any new and better combinations. In other words, such a remark means that the proportion of bad genes and good genes is the same in our present-day livestock as it was 100 years ago. Such a statement can be neither proved nor disproved in terms of the actual genes, and, because records of average accomplishment are totally lacking for the old animals and not very numerous for the present ones, and because nutritional and other environmental conditions have undergone such revolutionary changes, the statement can neither be proved nor disproved in terms of records. Crude as may have been our tools of selection, the writer is of the opinion that considerable progress has been made. And he is also of the opinion that the average merit of our animals can now be fairly speedily enhanced, because the basic principles of hereditary transmission are now known.

In the first chapter we sketched briefly the known history of animal breeding. Tablets and monuments from early Egyptian and Babylonian civilizations of 5,000 years ago depict very good types of cattle, sheep, and dogs, and it is known that these peoples used the ass as a beast of burden. The ancient Greek and Roman civilizations also had well-developed arts of agriculture and animal husbandry. During the Middle Ages there were undoubtedly local varieties of animals of good individual merit, but this period is noteworthy from our standpoint mainly as the time when the Arabian horse and the Merino sheep were developed. When Robert Bakewell started farming at Dishley in 1760, the real foundations of our present-day breeds began to be laid, and during the next 100 years practically all the breeds of livestock now found in America were developed. Then, roughly from 1860 to 1900, the breed associations for pedigreeing, protecting, and promoting the various breeds were established, the whole of the above process taking place before the principles underlying reproductive physiology and hereditary transmission were known, although spermatozoa had been discovered by Leeuwenhoek and Ham in 1677 and the ovum by von Baer in 1820. During all this period men had to breed by rule-of-thumb methods, and it is likely that magic and superstition played a large part in breeding operations.

Pre-Mendelian Plant Breeding.[1]—Conditions were very similar in the domain of plant breeding, good varieties of plants having existed and having been continuously improved since the remotest time. A German, Camerarius, discovered the sexual nature of plants in 1694, and in 1717 an Englishman, Fairchild, reported the first artificial plant hybrid. This

[1] See Cook, R., A Chronology of Genetics, *U.S. Dept. Agr. Yearbook*, 1937, pp. 1457–1477.

was followed by extensive work in crossing plants during the next 50 years, climaxed by Kölreuter's work in Germany in the 1760's. During the next 100 years, plant hybridizers discovered and reported the occurrence of dominance, recessiveness, segregation, hybrid vigor, and unit characters, but these isolated facts were not synthesized into a pattern of principles of inheritance, and the statistical relations indicating the uniformity of the behavior of the hereditary units were not recognized. The cell theory was advanced by Schleiden and Schwann in 1838. The decade 1840–1850 saw the beginning of the progeny testing of plants by Vilmorin, the figuring of the chromosomes by Hofmeister, the enunciation of the general principle of the continuity of the germ plasm by Owen, and the observation of actual fertilization of the egg by the sperm in seaweed by Thuret. In 1858, Virchow finally disposed of the old conception of spontaneous generation by means of his pronouncement, *omnia cellula e cellula* (every cell from a cell).

Then within a period of 7 years two of the most famous works of all time came off the press: Darwin's "Origin of Species" in 1859 and a paper by Mendel, "Plant Hybridizations," in 1866. The former created an immediate sensation, the latter, although it contained a clear and concise treatment of the basic principles of inheritance with practically perfect statistical results to buttress them, lay unnoticed for 34 years.

During these years great advances were made in the field of cytology. Hertwig proved in 1875 that fertilization consisted of the union of male and female pronuclei, which established the equal importance of both parents in hereditary transmission of potentialities; Flemming reported the splitting of the chromosomes in 1879; van Beneden the reduction of the number of chromosomes to one-half in the germ cells in 1883; Hertwig, Strasburger, Kölliker, and A. Weismann in 1884–1885 independently and practically simultaneously identified the cell nucleus as the basis of inheritance; and in 1888 the chromosomes were named by Waldeyer.

In the field of the practical, the progeny test in plant breeding was further developed, trap-nesting of poultry begun, and the Babcock test for determining the butterfat percentage of milk discovered. In 1891, Hays proposed the centgener method of progeny testing as the only adequate method for determining the genetic make-up and breeding worth of an individual. Statistical treatment of variation by means of correlation was devised by Galton in 1886, and the standard-deviation technique for determining the significance of deviations from theoretical perfection was developed by Pearson in 1898.

Breeding Advance since 1900.—With the independent rediscovery of the basic principles of inheritance by De Vries, Correns, and von Tschermak in 1900 and the bringing to light of Mendel's original work, a new

impetus was given to both the scientific and practical aspects of plant and animal breeding. These principles were demonstrated in animals by Cuenot in 1902 and in man by Davenport in 1904. The interrelations between the behavior of the chromosomes cytologically and the transmission of characters genetically was shown by Sutton in 1903, and the mechanism of sex determination suggested by McClung in 1902 was confirmed by Stevens and Wilson in 1905. The term *genetics* was coined by Bateson in 1906, and the theory of the gene was developed by Morgan and his collaborators at Columbia University in 1910, based upon experiments with the pomace fly, *Drosophila melanogaster*, which has a generation in 10 days numbering up to 400. Following the lead of Shull and East, many inbreeding and crossbreeding experiments were begun both to test and amplify the genetic theory and to try to develop true-breeding strains of both plants and animals. A host of discoveries of chromosome behavior in inheritance have developed since 1910, linkage, crossing over, the nature and production of polyploids, linear order of the genes, interference, limitation of the linkage groups, position effects, the function of inbreeding in reducing heterozygosity, the lethal action of certain genes, etc., the details of which we will meet in later chapters. Finally in 1927 came the artificial induction of mutations by X rays (Muller) and in 1933 the complete unification of cytology and genetics through Painter's work with the giant chromosomes found in the salivary glands of larval Drosophila.

The possibilities inherent in the application of genetic principles to the improvement of both plants and animals have become especially recognized since about 1920. In plants, many new varieties have been made to order, and "hybrid corn" is now used extensively throughout the corn belt. In animals we have again centered our attention on the basic fundamentals of proving sires by means of their progeny, as Bakewell did in the eighteenth century and as Varro suggested to Roman farmers in the first century B.C.

Genetics, or the science of breeding, has had a phenomenal development since 1900. The earliest characters studied were the most obvious external ones, such as color, horns, etc. This led some to expect that all animal characters would follow some such simple pattern of inheritance, and as a consequence many unjustifiable claims were made relative to the easy and rapid revolution in breeding practices soon to be achieved by means of genetics. The basic principles of inheritance have been revealed by means of the experimental breeding of small inexpensive and rapidly breeding forms. The detailed mode of inheritance of most of the commercially valuable characters of our larger forms of livestock are still unknown. Our lack of knowledge regarding the mode of inherit-

ance of commercially valuable characters doubtless rests in part upon the fact that each parent produces only a small number of progeny, but probably of more importance is the fact that such characters are of a quantitative nature with many pairs of genes being involved in their inheritance. The specific nature of the inheritance of quantitative characters is still far from understood even in rapidly reproducing forms such as Drosophila, mice, and many plants where they have been studied extensively.

Fortunately, we do not need to wait for the details to be discovered any more than we needed to wait until the exact nature of electricity should become known before putting it to use. Knowledge of the broad basic principles, which we now have, will expedite breeding progress tremendously whenever we develop the ingenuity and desire to really put it to work.

The student should keep in mind during the reading of the next few chapters that the facts revealed by means of breeding experiments furnished the materials on which various portions of the theory of inheritance are based rather than the reverse of this process. Breeding facts supply the materials from which a working hypothesis can be formed. Further experiments are then devised to test the validity of the hypothesis. Such is the *modus operandi* of science.

Problems of Genetics.—The principal problem of genetics is of a threefold nature. Obviously the geneticist is primarily concerned with the mode of transmission of potentialities from parent or other ancestor to offspring. The solution of this problem is of scientific interest, but much more so is it of practical concern. On its solution hinges our ability to create plants and animals of a more useful type, more useful in terms of efficiency, productivity, longevity, as well as those more able to withstand the onslaughts of drought, disease, and insect pests. With this knowledge, man can, if he wishes, gradually eliminate various sorts of defectives from his own ranks.

In addition there are two other problems facing geneticists. One of these has to do with the physicochemical nature of the gene itself, which, when solved, may throw considerable light on the origin and development of life in an evolutionary sense. The third problem has to do with the developmental and functional processes of the organism, the forces and interactions between the genes, the cytoplasm and the environment leading to the organization of the material into a specific pattern.

Problem of Physicochemical Cause.—An elaboration upon the physicochemical entities that probably function in the transmission of similarities or the rise of differences belongs in the fields of chemistry and cytology. Much progress has already been made here, and it is through the cytologi-

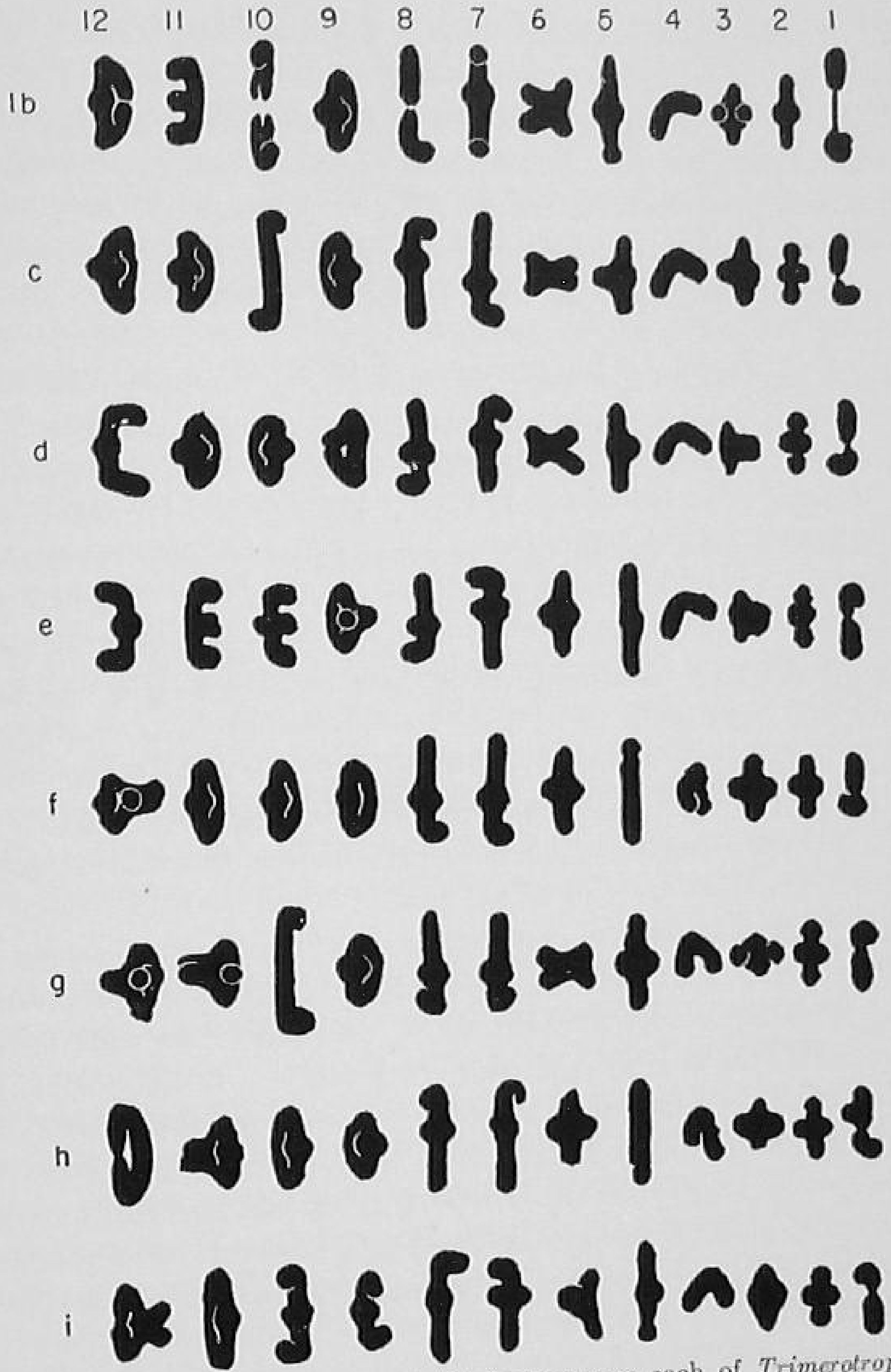

FIG. 86.—Eight chromosome groups of 12 chromosomes each of *Trimerotropis*. (*From Morgan after Carothers, Physical Basis of Heredity, J. B. Lippincott Company.*)

cal behavior of chromosomes that the foundation for present-day genetics has been laid. Research has established the fact that the behavior of the chromosomes in gametogenesis exactly fits the observed appearance and distribution of characters in the developed individual. This is an accomplishment of the greatest moment. There is no doubt but that the chromosomes constitute the main "bridge of inheritance." The function of the cytoplasm of the cell is not to be overlooked, but it seems to be no more than secondary to the nuclear material contained in the

chromosomes. In the case of certain plants, there is genetic evidence that seems to indicate that certain chlorophyll characteristics of these plants are controlled by plastids which are distributed in a more or less haphazard fashion to the daughter cells, but this is not a contradiction in any sense of Mendelian inheritance, but only an additional type of inheritance. During the past few years there has been much interest in the possibility that genes or genelike substances may be able to duplicate themselves in the cytoplasm and be passed on at cell division. Positive proof for the existence of true "cytogenes" has not been advanced, however.

Many investigations are now in progress in an attempt to explain the nature of the gene. Genes are probably complex nuclear proteins which contain several types of nucleic acid. The genes themselves are arranged in a definite order in morphological structures which we call chromosomes. The physicochemical processes which are involved when the chromosomes and genes duplicate themselves prior to and during mitosis are incompletely understood. For our purposes in this text, we can regard these changes as complex biochemical processes which are carried on by nature with rather remarkable uniformity. Whereas relatively complex steroid and carbohydrate compounds have been synthesized in the laboratory for many years, even the simplest proteins remain to be produced outside living organisms.

During the past decade, many studies with lower organisms, principally the mold *Neurospora* and certain other microorganisms, have revealed much information in regard to genetic make-up of the organism and cellular function. For example, mutant strains of *Neurospora* each failing to produce a specific enzyme are unable to synthesize certain specific vitamins of the B-complex or amino acids. Other strains synthesize these materials readily. It is now known that these functions are dependent upon the presence of specific genes. The selection of strains of organisms for the maximum production of important antibiotics such as penicillin or aureomycin and even the newest of the vitamins, the animal protein factor, are an outstanding example of the role of genetics in human welfare. In each case there is good evidence that the biochemical principles involved are related to specific genes.

A complete delineation of the chemical make-up of genes and chromosomes may not aid immediately in any practical manner in creating better organisms, but the knowledge for its own sake will be very gratifying when it can be achieved, and future generations may put it to practical use.

Problem of Developmental Organization.—Another great problem is that of hereditary specificity and developmental organization of the individual. In other words, what is the mechanism resident in the

fertilized ovum "which impels it to follow in each case a definite line of development"? This problem, unlike that of the nature of the gene and transmission, which deal with the germ plasm, is concerned with the somatoplasm. The method of attack here is the embryological one—not the old descriptive embryology with its manifest limitations in this respect, but the new experimental embryology, "using the term in its widest sense to include the study of such phenomena in regeneration, regulation, growth, etc." This is primarily a study of ontogeny, and it will eventually fill the void now existing between the original zygote with its content of hereditary determiners and the fully developed adult exhibiting the characteristics for which determiners were present in the zygote.

A great deal of intricate experimental embryological research is beginning to shed light on this problem. Transplantation and regenera-

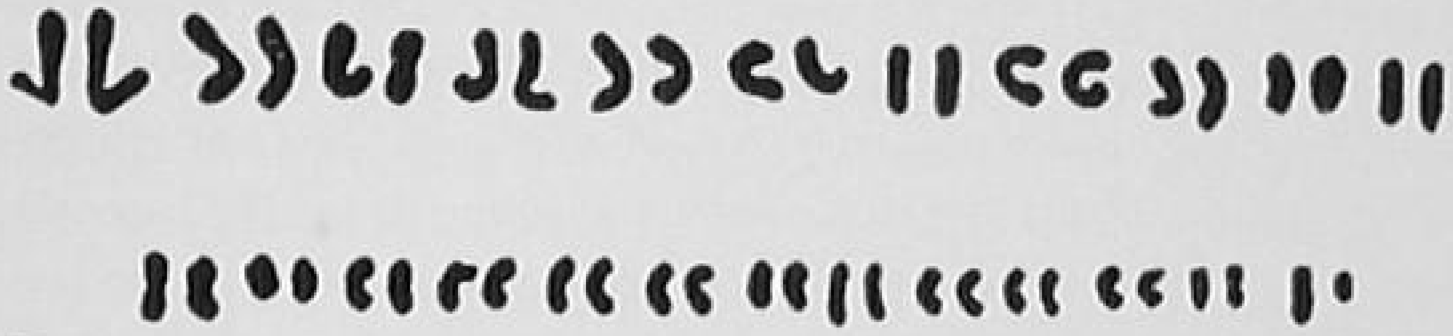

FIG. 87.—The 24 pairs of chromosomes in human male. (*P. Popenoe, The Child's Heredity, Williams & Wilkins Company.*)

tion techniques have shown that various parts of the body act as organization centers, elaborating hormonallike products which provide the patterns for further development. Belly tissue of the young frog embryo, which, if left in place, would have produced skin, will, if transplanted early enough to the region of the jaw, produce a normal frog jaw. If, however, it is transplanted to the jaw region of a salamander, it will as formerly produce jaw tissue, but it will be the jaw of a frog because of the frog genes that it contained. Development, therefore, is due primarily to the genes and perhaps secondarily to the interaction of the developing tissues with other nearby tissues, which, of course, have been gene-determined. Also the amputation of half a limb of a salamander will be followed by a complete regeneration of a normal limb, bone as well as muscle and nerves, which indicates a substance in the cells of the stump capable of directing the normal development of the tissues that spring from it.

Problem of Mode of Transmission.—There are two methods of studying the manner in which characteristics are transmitted from one generation to the next. They are (1) by studying the ancestors of certain individuals or (2) by studying the progeny of certain individuals. The former, or ancestor study, may be carried on by means of biometry or by means of data recorded in purebred herd books. The progeny study

is the experimental or Mendelian method, in which the matings are planned, and the study may have a statistical basis. Inquiry will now be made into these methods of genetic research, bearing in mind that in this field, particularly, environmental conditions must be carefully controlled so that the observed results may justifiably be attributed to the make-up of the germ plasm.

The statistical method of attacking the problem was originated by Sir Francis Galton, later developed by Karl Pearson, and is known today as *biometry*.

It is a most useful tool in the hands of the analytical geneticist. Its function is to measure the degree of resemblance between related individuals and to express the result in numbers. As pointed out by Pearl, the weakness of the method as a means of research lies in two facts: (1) it is largely a method of description and does not attempt to give the cause of the events, and (2) because biometry gives the degree of resemblance between parent and offspring, and because heredity is a cause of the resemblance, the biometrical method (correlation) measures the degree or intensity of inheritance. As Pearl points out, heredity is not the sole cause that can lead statistically to a significant correlation between parent and offspring. "Anything whatsoever which tends to bring about local group differentiation within the sample included in the table will tend to produce the same result, altogether independent of any genetic relationship or the absence of it."

With its limitations and dangers kept in mind, biometry, properly used, is a valuable agent in the study of genetics.

Herd books and production records of livestock may be made to yield valuable information on the problem of hereditary transmission. With the aid of such records, the manner of transmission of superficial characters, such as color markings, set of ears, and so on, as well as the deeper lying functional activities, such as speed, milk production, etc., may be investigated. This method can be criticized as being descriptive rather than experimental, and in it there is also the danger that an investigator may not have access to all the relevant facts. These records are now beginning to yield information that should prove of great value to practical breeders by explaining how certain traits are inherited and possibly also by showing the falsity of timeworn beliefs.

The two preceding methods have dealt with the ancestors. The following will be concerned with progeny. This is the experimental-breeding or pedigree-culture method, which Mendel used so successfully. He succeeded in discovering the basic plan of hereditary transmission, because he reduced his problem to its simplest form and studied one pair of contrasted characters at a time. Like the Galtonian, this method is

also statistical. In general, it consists of producing pure races, crossing them, mating the hybrids, and ascertaining the ratios in the F_2 and later generations. This method has also resulted in the establishment of Johannsen's pure-line theory and De Vries's mutation theory. The former of these has been defined as "all the progeny of a single self-fertilized individual." Such individuals eventually give rise to inbred strains that are homozygous genetically but with fluctuating variations in each inbred line. These variations are probably due largely to environmental conditions and not to germinal variations. In other words, this points to the static character of the germ plasm, or its conservative nature.

The mutation theory suggested by De Vries, on the other hand, postulates sudden heritable changes in the genes. This provides one means of heritable variation and points to the dynamic character of the germ plasm, or its progressive nature.

Finally the organism itself will often provide a partial index to its genetic make-up. If a character behaves as a recessive, we know the genetic make-up of an animal evidencing this character (for this character). This is true also in a case where dominance is lacking, for the homozygous dominant (AA), the heterozygote (Aa), and the homozygous recessive (aa) will all evidence different expressions of the character. If the character shows complete dominance, however, we will be unable to distinguish between AA and Aa individuals.

In animal breeding, our aim is the creation of desirable and efficient animals that will of necessity transmit their own desirable qualities to a high percentage of their offspring. We want all the evidence that we can get regarding the likelihood that our desirable animals will be good transmitters. Summarizing the above discussion we can get this information from

the individual itself

↙ ↘

its progeny its ancestors

Genetics and the Practice of Breeding.—The practice of breeding is older than history. Its method is selection, and its accomplishments legion. It has produced fast, fancy, and farm horses; increased the yield of milk from a few hundred to 41,000 lb. annually; and has produced the food that has enabled man literally to conquer his world. Genetics acknowledges gladly the achievements of empiricism and seeks the reason "why." The method of practical breeders has always been that of trial and error, and of necessity there has always been a goodly share of the latter. The greatest service that genetics can render to the practice of breeding lies in its ability to analyze and to provide logical explana-

tions. This will inevitably result in the sifting of the true from the false, a service of no mean value and one which is being fulfilled rapidly. If genetics did no more than unearth the principles underlying breeding and post "no-passing" signs at the head of all the blind alleys, it would expedite successful breeding to a marked degree.

However, knowledge gained through genetic studies has already provided new methods that will lead more quickly and surely toward the goal of more beautiful form and more efficient function. Detailed knowledge of the mode of inheritance of most of the characteristics exhibited by higher animals is still unknown and from the very nature of the problem is difficult, though genetics bids fair to furnish the solution. When this has come about and the principles are thoroughly understood, genetics will have proved itself merely the handmaid of animal breeding, to which it will have rendered a valuable service in successfully and firmly fitting into place the keystone of all breeding operations, "rational selection."

To be successful in breeding better livestock, a person should first of all love to work with animals. Next comes the necessity for a thorough knowledge of the history, accomplishments, and shortcomings of one's particular breed. Practice in livestock judging bulwarked by a knowledge of anatomy and physiology and by experience gained through study of finished carcasses in meats courses should also prove to be very useful. Finally, courses in veterinary hygiene and science, together with the materials presented in the books dealing with animal breeding, should complete one's initial training for animal-breeding work with actual experience in the field serving as a continuing source of enlightenment and inspiration.

Summary.—This chapter serves as a general introduction for our consideration of genetics, which, as we have seen, is concerned with similarities and differences exhibited by related organisms. We have laid particular emphasis on the chromosomes as "the bridge of inheritance," but we should be careful not to overlook the large part played by both environment and training in bringing any inherited character to its full fruition. We traced very hurriedly the long history of both plant and animal breeding and saw how the occasionally observed facts of inheritance down through the ages were finally fitted together into a complete and complex whole by Mendel and his successors. The three principal types of problems that genetics and related sciences are trying to solve were indicated as well as a preview of the methods now being used to effect solutions. Finally, we listed practical prerequisites for the scientific animal breeder and indicated the role of genetics in the practical field of animal husbandry.

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CHAPTER XII

THE PRINCIPLES OF HEREDITY

Men have been breeding plants and animals for many thousands of years. In the earliest stages of breeding, the main purpose was probably that of seizing upon favorable variations in order to try to improve both plant and animal species. By allowing these favorable variates to have many offspring and less desirable ones to have few or none, a slow, steady improvement ensued. The question was, "how" can we secure better plants and animals to serve our human needs?

Early man, like children of today, was probably randomly curious. He wondered in a vague way about the stars, his own whence and whither, etc. The early Egyptians and, later, the Greeks began to develop a system of experimental observation and inquiry, but later events put a stop to these beginnings. Up until about the year 1500, authoritarianism (believing what others had said) and the fear of religious persecution succeeded in quite thoroughly throttling any intelligent curiosity. Gradually these shackles were unloosed, and man began to add experimentation to speculation. This was the beginning of the age of enlightenment. Copernicus, Brahe, Kepler, and Galileo soon proved through mathematical calculations and observation that the earth, far from being the center of the universe, was in fact but one of several relatively tiny specks which revolved around a rather puny star, our sun. Newton soon combined the mathematical physics of Descartes and Galileo's law of falling bodies into the gravitational theory of an orderly and immense universe in which nothing is left to chance or caprice.

These discoveries, deductions, and syntheses finally proved that old authorities were not infallible, that observation and common sense had their limitations, because things were not always what they seemed to be and, most important of all, man's own reason backed by observation, calculation, and experiment was the most trustworthy guide available.

Eventually this intellectual curiosity was directed toward the world of living things. Man began to experiment to try to find out "why" the results of certain matings yielded certain results. This was especially true in the plant kingdom, in which many men carried on plant hybridization experiments in attempts to fathom nature's secrets in the transmission of characters from parent to offspring. In 1694, Camerarius

published a work which showed that plants were sexual organisms. In 1717 occurred the production of the first artificial plant hybrid by Thomas Fairchild. The work of Spallanzani in the eighteenth and Pasteur in the nineteenth century proved the old idea of spontaneous generation to be a fallacy; Schleiden and Schwann discovered the cellular nature of plants and animals; and Darwin established the validity of the process of organic evolution.

Finally, breeding experiments with peas carried on from 1857 to 1865 by an Austrian monk, Johann Gregor Mendel, revealed some of the basic

Fig. 88.—Gregor Mendel, the discoverer of the laws underlying inheritance.

principles of hereditary transmission. There had been many other plant hybridizers before Mendel, but he was the first to attack the problem on a large enough scale and in such a thoroughgoing way that it became possible (1) to determine the number of different forms under which the offspring of hybrids appeared, (2) to arrange these forms with certainty according to their separate generations, and (3) to ascertain definitely their statistical relations. In 1866, he published a report of 8 years' hybridization experiments, though 34 years elapsed before the validity of his pioneer work was established. Mendel, like many other men who have thought ahead of their time, died before the results of his splendid pioneering were appreciated.

Like many other natural phenomena, this matter of inheritance yielded to a fairly simple interpretation, and Mendel's success was due in large

measure to the fact that he reduced his problem to its very simplest form by studying one pair of contrasted characters at a time, coupled with the fact that he happened to work with characters which were determined by genes carried in different chromosomes and which therefore assorted independently. Mendel's discovery was duplicated in 1900 by three botanists, DeVries, Correns, and von Tschermak, and this led eventually to the discovery of Mendel's original paper.

Mendel's work laid the basis for the later establishment of two of the general laws of inheritance, *viz.*, those of segregation and of independent assortment. To these have been added, since 1900, the following: linkage, crossing over, linear order, interference, and limitation of the linkage groups. Some of these later principles are in a sense antithetical to the original Mendelian principle of independent assortment, but for the sake of clarity and unity all the phenomena of inheritance, based on the reactions of genes, are generally known under the collective term *Mendelism.*

MENDELIAN TERMS

The following are some of the terms now in general use in referring to Mendelian phenomena.

Unit Characters. Any characters of any organism that behave as a unit in inheritance—plant size in peas, horns in cattle, etc.

Genes. The units of inheritance that probably react together and with the cytoplasm, and these two with the environment to make patent the organism's latent potentialities.

*Allele**. Mendelian characters are inherited in alternative pairs (or series). These alternative forms of a gene, which are located at the same point on each one of a pair of chromosomes, are called *alleles, e.g.,* albinism (recessive), normal pigmentation (dominant); horns (recessive), hornlessness (dominant). (Allelomorph, allelic, adjective—variants.)

*Dominant**. A character, possessed by one of the parents of a hybrid, which is manifested in the hybrid to the apparent exclusion of the contrasted character from the other parent (the recessive). Thus in a cross of green- and yellow-seeded peas the first generation has yellow seeds. Yellow is dominant and green is recessive, being transmitted but not appearing in the presence of the factor for yellow.

Hybrid. The individual that arises from crossing parents which are pure for certain different characteristics. Crossing tall (*TT*) on dwarf (*tt*) peas produces a hybrid (*Tt*).

Monohybrid. A hybrid that is heterozygous for one pair of allelic genes.

* Definitions marked with an asterisk taken from "Glossary of Genetic Terms," *U.S. Dept. Agr. Yearbook,* 1936, pp. 153–164.

Dihybrid. A hybrid that is heterozygous for two pairs of allelic genes.

Trihybrid. A hybrid that is heterozygous for three pairs of allelic genes.

Phenotype. The expressed character (or sum of all the characters) of an organism; *e.g.*, if, in peas, genes for both the tall and the dwarf characteristics (T and t) are present, the pea grows tall, and therefore belongs to the tall phenotype.

Genotype. What an organism actually is as determined by its germ plasm; *e.g.*, TT and Tt are both tall peas, therefore, the same phenotype, but because of their different genotypic constitutions will transmit differently and therefore belong to different genotypes.

*Heterozygote**. An organism to which its two parents have contributed unlike genes with respect to any given allelic pair governing contrasted characters, and which in turn produces two kinds of germ cells with respect to the character. (Heterozygous, adjective.)

*Homozygote**. An organism whose parents contributed to it a similar member of any given pair of genes, and whose germ cells are therefore all alike with respect to the genes for that character. (Homozygous, adjective.)

*Race**. A group of individuals having certain characteristics in common because of common ancestry—generally a subdivision of a species.

Gamete. A reproductive cell of either sex; a sperm or ovum.

*Heredity**. The resemblance, derived from the ancestry, among organisms related by descent.

P. Parental generation.

F_1. First hybrid generation—made by crossing $P \times P$.

F_2. Second hybrid generation—made by crossing two F_1 hybrids.

*Variation**. In biology, the occurrence of differences among the individuals of the same species or variety.

Haploid. Single; referring to the reduced number of chromosomes in the mature germ cells of unisexual organisms (n).

*Diploid**. Having two sets of chromosomes. Body tissues of higher plants and animals are ordinarily diploid in chromosome constitution ($2n$).

*Polyploid**. Normal body cells of the higher plants and animals have two sets of chromosomes. Polyploids are forms having three or more of these basic chromosome sets (3 or more n).

*Heteroploid**. An organism characterized by a chromosome number that is not a multiple of the basic haploid number.

Physical Basis of Inheritance.—In Chap. III we presented a short discussion of chromosomes and genes, and in Chap IV and V we outlined the mechanisms involved in the production of sperm and ova and the behavior of the chromosomes during these processes.

The chromosomes are sometimes called the "bridge of inheritance" since they serve as the sole connecting link between each two succeeding generations. The ultimate indivisible units of inheritance are the genes. While genes are units, they do not behave as such because many of them are joined together in a linear series and this group of genes is called a chromosome. The chromosomes consist of a definite number for each species of plant and animal.

Any individual is duplex in its chromosome make-up (except for the sex chromosome in the male in most higher organisms). The chromosomes are paired in each body cell, one member of each pair having been supplied by each parent. When an organism produces germ cells, however, only one member of each pair is found in each resulting gamete. In this fashion, the number of chromosomes is reduced to one-half in each gamete, and the normal species number of chromosomes is again restored when an egg and sperm unite at fertilization.

The Essence of Mendelism.—One of Mendel's experiments involved the crossing of tall and dwarf peas, and he found that all the offspring grew tall, because in this species tall growth is dominant over dwarf. When these F_1 hybrids were crossed, the resulting F_2 generation consisted of tall peas and dwarf peas in the ratio of 3:1. The following diagram should make this clear:

TT — pure tall parent — *T* — pollen after reduction

tt — pure dwarf parent — *t* — ovules after reduction

Tt F_1 hybrid (tall) {either ovule fertilized by either pollen}

T *t* — pollen of hybrid after reduction

T *t* — ovules of hybrid after reduction

TT *Tt* *Tt* *tt*

tall 3 : dwarf 1

The *TT* peas are pure for tallness and will produce all tall offspring. The same holds true for the *tt* peas in respect to dwarfness. The two *Tt* peas are phenotypically tall, but carry the factor for dwarfness *t* as a recessive. Two of these crossed would again give:

T *t*

T *t*

TT, *Tt*, *Tt*, *tt*, etc., ad infinitum

This 3:1 ratio is phenotypic, the genotypic ratio being 1:2:1. This was the gist of Mendel's work; *viz.*, starting with parents pure for some contrasted character, hybrids would be produced in the F_1 that looked like the dominant parent; and, in the F_2, ¼ of the population would be pure for one grandparental characteristic, ¼ pure for the other grandparental characteristic, and ½ would carry both factors and resemble the dominant parent.

Mendel's Hybridization Experiments.—It is of importance to know how far Mendel's results and later experiments meet mathematical expectations. For this reason it will be well to consider both Mendel's original work and some later experiments. The point at issue is whether Mendel discovered an interesting restricted phenomenon in peas or a universal law of inheritance.

Mendel secured some 34 more or less distinct varieties of peas and, before beginning his own experiments, subjected them to a 2-year trial to ascertain whether or not they would breed true to type. Knowing that some characters of plants are transmitted unchanged to the hybrids and their progeny and that one of each pair of contrasting characters of two plants appeared in the hybrid as the dominant character, whereas the other (recessive) reappeared in the progeny of the hybrid, Mendel planned his experiment to observe and record the proportion of each pair of differentiating characters in the succeeding generations of hybrids and to deduce the law according to which they appear in the successive generations.

Mendel selected the following seven pairs of contrasted characters for study:[1]

1. The difference in the form of the ripe seeds. These are either *round* or *roundish*,[2] the depressions, if any, occur on the surface, being always only shallow; or they are irregularly angular and deeply wrinkled.

2. The difference in the colour of the cotyledons. The albumen of the ripe seeds is either *pale yellow, bright yellow, and orange coloured*, or it possesses a more or less intense green tint.

3. The difference in the colour of the seed coat. This is either white, with which character white flowers are constantly correlated; or it is *grey, grey brown, leather brown*, with or without violet spotting, in which case the colour of the standards is violet, that of the wings purple, and the stem of the axils of the leaves is of a reddish tint. The grey seed coats become dark brown in boiling water.

4. The difference in the form of the ripe pods. These are either *simply inflated*,

[1] Castle, W. E., "Genetics and Eugenics," p. 317, Harvard University Press, Cambridge, Mass., 1916.

[2] In each case the dominant character is italicized.

not contracted in places; or they are deeply constricted between the seeds and more or less wrinkled.

5. The difference in the colour of the unripe pods. They are either *light to dark green* or vividly yellow, in which colouring the stalks, leaf veins and calyx participate.

6. The difference in the position of the flowers. They are either *axial*, that is, distributed along the main stem; or they are terminal, that is, bunched at the top of the stem and arranged almost in a false umbel; in this case the upper part of the stem is more or less widened in section.

7. The difference in the length of the stem. The length of the stem is very various in some forms; it is, however, a constant character for each, in so far that healthy plants, grown in the same soil, are only subject to unimportant variations in this character.

In experiments with this character, in order to be able to discriminate with certainty, the *long axis of* 6 *to* 7 *feet* is always crossed with the short one of ¾ to 1½ feet.

The results of segregation in the F_2 in those seven series of experiments by Mendel are shown in Table 18.

Mendel was dealing with strictly contrasting characters and got no intermediate or blending forms. The matter of personal bias was therefore obviated. The phenotypic ratio that Mendel secured in the F_2 with each pair of contrasted characters was in no case significantly different from 3:1. Many other investigations of single contrasting characters have yielded a similar 3:1 phenotypic ratio in the F_2.

Mendel carried some of the descendants of the above hybrids along through four to seven generations and reported that "no departure from the rule has been perceptible."

Table 18.—Summary of Mendel's Experiments with Peas

Number	Character contrast	Number in F_2	Dominants	Recessives	Ratio
1	Form of seed	7,324	5,474	1,850	2.96:1.00
2	Color of cotyledons	8,023	6,022	2,001	3.01:1.00
3	Color of seed coats	929	705	224	3.15:1.00
4	Form of pod	1,181	882	299	2.95:1.00
5	Color of pod	580	428	152	2.82:1.00
6	Position of flowers	858	651	207	3.14:1.00
7	Length of stem	1,064	787	277	2.84:1.00
Totals		19,959	14,949	5,010	2.99:1.00

He also made crosses of individuals differing simultaneously in two and in three characteristics and found the same underlying principle

active; *viz.*, the F_1 hybrids looked like the sum of the dominant characters put in by both parents, and in the F_2 all the characteristics were recombined into all the possible combinations.

The Mendelian Theory of Inheritance.—The essence of Mendel's work is summed up in this statement[1] of Mendel's.

> The results of the previously described experiments led to further experiments, the results of which appear fitted to afford some conclusions as regards the composition of the egg and pollen cells of hybrids. An important clue is afforded in Pisum by the circumstance that among the progeny of the hybrids constant forms appear, and that this occurs, too, in respect of all combinations of the associated characters. So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilizing pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilization of pure species. We must, therefore, regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in one plant, or even in one flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.
>
> In point of fact, it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers.

Mendel's results were published in 1866, and his paper was discovered by De Vries, a Dutch botanist, in running down the literature on plant hybridization following his own experiments with the evening primrose, from which work he formulated his theory of mutations and his law of "the splitting of hybrids." Apparently Correns in Germany and von Tschermak in Austria discovered the latter principle at about the same time.

The principles evidenced by the work of Mendel, De Vries, Correns, and von Tschermak have since been named *segregation* and *independent assortment*.

1. *Segregation.* A new individual arises from the union of a male and a female gamete that contain a sample half of the complete genetic material of each parent, *i.e.*, one or the other member of each pair of chromosomes. Each parent contributes a complete haploid set of chromosomes to each of its offspring. When this new individual matures

[1] Castle, *op. cit.*, p. 332.

and begins to produce germ cells, the latter go through the process of reduction, at which time the chromosomes put in by the parents segregate or separate out from each other, one member of each pair going to each of the secondary germ cells, in all the possible combinations. This principle is illustrated in the tall- and dwarf-pea cross, the pollen or

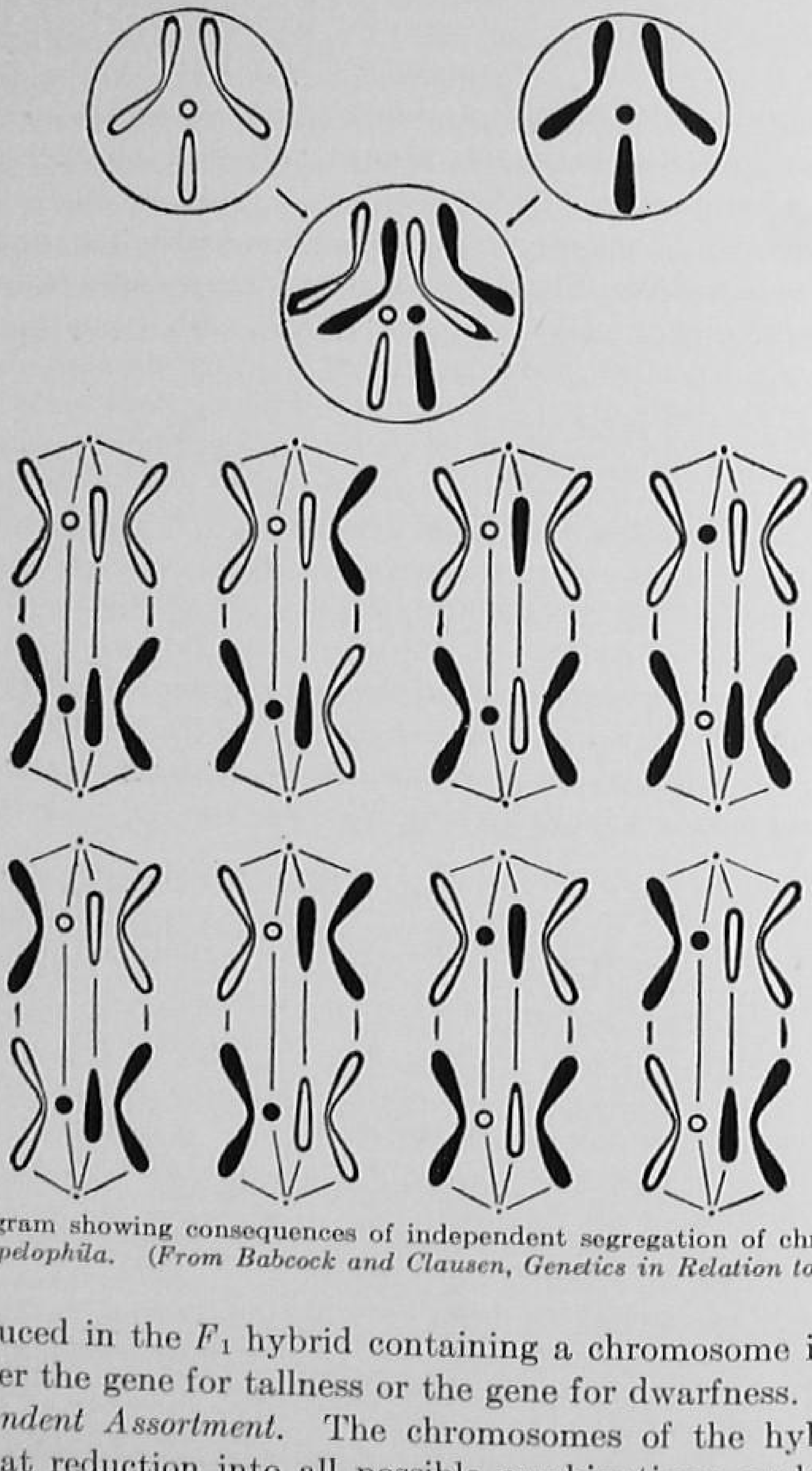

Fig. 89.—Diagram showing consequences of independent segregation of chromosomes in *Drosophila ampelophila*. (*From Babcock and Clausen, Genetics in Relation to Agriculture.*)

ovules produced in the F_1 hybrid containing a chromosome in which is located either the gene for tallness or the gene for dwarfness.

2. *Independent Assortment*. The chromosomes of the hybrid assort themselves at reduction into all possible combinations, each germ cell necessarily having one member of each pair of chromosomes. With one pair of chromosomes, two genetically different germ cells are produced

(2^1); with two pairs of chromosomes, four genetically different germ cells are produced (2^2); with three pairs, eight genetically different germ cells are produced (2^3); etc. Chromosomes and genes were unknown in Mendel's day. He did not speak of them but rather in terms of the characters of his plants. Since, however, all of the characters in peas with which Mendel worked were apparently determined by factors (genes) located in different chromosome pairs and no two of them by genes in the same pair of chromosomes, Mendel was able to postulate the most important principle of inheritance, independent assortment, which actually applies to chromosomes and not, as Mendel perhaps thought, to characters.

Segregation and independent assortment constitute two of the basic principles of inheritance. For independent assortment or distribution of characters, the pairs of contrasting characters considered must be determined by genes carried in different chromosomes. If the two or more pairs of contrasted characters were determined by genes carried in the same chromosome, they would not be expected to assort independently but rather to remain linked together. Linkage relations will be discussed later.

Monohybrid Crosses.—A monohybrid is a hybrid that is heterozygous for one pair of allelic genes. When we cross a homozygous tall parent (*TT*) with a homozygous dwarf (*tt*) we get a monohybrid (*Tt*). If two of these monohybrids are crossed, we get a ratio of 3 tall : 1 dwarf offspring. For an explanation of these breeding facts we assume that one parent has the genes for tall growth and the other parent the genes for dwarf growth at similar loci in homologous chromosomes, and that these genes are both present in the monohybrid but separate or segregate when the monohybrid produces germ cells with the haploid number of chromosomes. Remember, we have never seen these genes, and, if we could see them, they would have no labels. We get these certain results from certain crosses, and, knowing the general behavior of the chromosomes at gametogenesis, we use the simplest theory possible to explain the breeding results, in this case, one pair of genes.

Polled and horned cattle might be substituted for tall and dwarf peas and the problem worked out in the same way, the polled being dominant to the horned condition.

Dominance between alleles is not a universal phenomenon; *e.g.*, in a cross between a red and a white Shorthorn the F_1 are all roan.

red *RR* × *rr* white
germ cell *R* → *r* germ cell
F_1 → *Rr* ← a roan pattern (mixture of red and white hairs)

If we mate roans, we will get

Eggs	Sperm	
	R	*r*
R	*RR* red	*Rr* roan
r	*Rr* roan	*rr* white

or a phenotypic ratio of 1 red:2 roans:1 white, instead of the 3:1 phenotypic ratio that is evidenced when dominance between the genes is present. This 1:2:1 phenotypic ratio is also seen to be the genotypic ratio: in other words, we can tell by the appearance of these animals what their genotypes for color are. Lack of dominance is, therefore, seen to be an advantage, and dominance a disadvantage from a practical breeding standpoint, because the latter permits two or more genotypes to be masked under one phenotype.

Dihybrid Crosses.—A dihybrid is one that is heterozygous for two pairs of allelic genes. As an example, we can take the case of a cross between a homozygous smooth, black guinea pig (*rr BB*)[1] and a homozygous rough, white (*RR bb*), which would give the dihybrid heterozygous rough, black (rough and black behaving as dominants).

smooth, black *rr BB* × *RR bb* rough, white
germ cells *rB* *Rb* germ cells
↘ ↙
F_1 dihybrid *Rr Bb* heterozygous rough black

Mating two of these dihybrids together would mean that any egg could be fertilized by any sperm. These possibilities are best shown by means of the following checkerboard arrangement (Fig. 90).

When two of these F_1 dihybrids produce germ cells, spermatozoa or ova as the case may be, each germ cell will have the chromosome with the gene for either roughness or smoothness, *R* or *r*, and the chromosome with the gene for either black coat or white coat, *B* or *b*, because, being located in different chromosomes, the two pairs of genes assort independently. All the possible combinations of the four genes represented in the hybrid would be expected, therefore, both in the spermatozoa produced by a male as well as the ova produced by a female.

[1] The notation used in this book is based on using the capitalized first letter of the dominant character to represent the dominant gene and the corresponding small letter to represent the recessive gene. In this case rough and black are dominant, therefore *RR* (or *Rr*) = rough; *rr* = smooth; *BB* (or *Bb*) = black; *bb* = white.

Rr Bb × *Rr Bb*

Sperms	Ova			
	RB	*Rb*	*rB*	*rb*
RB	*RR BB*	*RR Bb*	*Rr BB*	*Rr Bb*
Rb	*RR Bb*	*RR bb*	*Rr Bb*	*Rr bb*
rB	*Rr BB*	*Rr Bb*	*rr BB*	*rr Bb*
rb	*Rr Bb*	*Rr bb*	*rr Bb*	*rr bb*

Fig. 90.—Checkerboard of the F_2 of a dihybrid cross of smooth black × rough white guinea pig.

In the above checkerboard the presence of at least one large *R* determines roughness, at least one large *B* determines blackness, otherwise the animal will be smooth and white. Segregation is an extremely important feature of inheritance, because through it something entirely new may be created. Starting with smooth, black and rough, white guinea pigs, something new, a smooth, white individual was created.

Figure 90 indicates that the following results have been secured.

9 rough blacks—at least one *R* and one *B*.
3 rough whites—at least one *R* and two *b*'s.
3 smooth blacks—two *r*'s and at least one *B*.
1 smooth white—two *r*'s and two *b*'s.

This is the usual dihybrid ratio, although there are several variations of it due to lack of dominance in one or both pairs of genes or to various forms of epistasis.

Similarly, if we mated a homozygous polled, black bovine to a horned, red one, we would get the results shown below.

polled, black *PP BB* × *pp bb* horned, red
germ cells *PB* *pb*
↘ ↙
F_1 dihybrid *Pp Bb* heterozygous polled, black

Experience has shown that the polled condition is dominant over the horned condition, and black color over red in cattle.

The genes for polled or horned and for black or red are apparently located in different chromosomes, because, when we mate dihybrids *Pp Bb*, we get a ratio of

9 polled blacks.
3 polled reds.
3 horned blacks.
1 horned red.

indicating that the germ cells containing genes *PB*, *Pb*, *pB*, and *pb* were produced in equal numbers by all these dihybrids.

The nine polled, black individuals are of the same phenotype but the nine are made up of

1 *PP BB*
2 *PP Bb*
2 *Pp BB*
4 *Pp Bb*

or four different genotypes in the same phenotype, and the only way to ascertain the different members of these four genotypes is through breeding trials. This brings to our attention a very important practical consideration, *viz.*, that we can't always tell by the appearance or performance of an animal, its phenotype, how it will transmit. The *PP BB* animal is polled and black and all of its offspring will be polled and black, because it must transmit both gene *P* and gene *B* to all its get. But the *Pp Bb* animals are also polled and black, but these animals may transmit the combinations of *PB*, *Pb*, *pB*, or *pb* genes to their offspring. One of the latter animals (*Pp Bb*) if mated to horned, red animals will get offspring as indicated below;

	PB	*Pb*	*pB*	*pb*
pb	*Pp Bb* polled, black	*Pp bb* polled, red	*pp Bb* horned, black	*pp bb* horned, red

whereas a homozygous polled, black animal, *PP BB* (germ cells all *PB*), if mated to horned, red animals will get all polled, black offspring, *Pp Bb*. The way in which an animal will transmit depends on its genotype, which may or may not correspond with its phenotype. The later chapters of this book on selection in horses, cattle, sheep, and swine will be devoted quite largely to a consideration of the procedures necessary to learn the genotypic make-up of our breeding animals.

A situation similar to the two dihybrid examples described above prevails in the inheritance of comb shape in poultry, but here the two pairs of factors influence only *one* characteristic instead of two. In this case *RR pp* birds are rose-combed, *rr PP* birds are pea-combed, and, when these are crossed, giving *Rr Pp*, the combs are walnut-shaped. Crossing two walnuts, *Rr Pp*, gives 9 walnuts, 3 rose, 3 pea, and 1 single comb, *rr pp*.

Trihybrid Crosses.—A trihybrid is one that is heterozygous for three pairs of allelic genes. The reader can now figure out for himself the

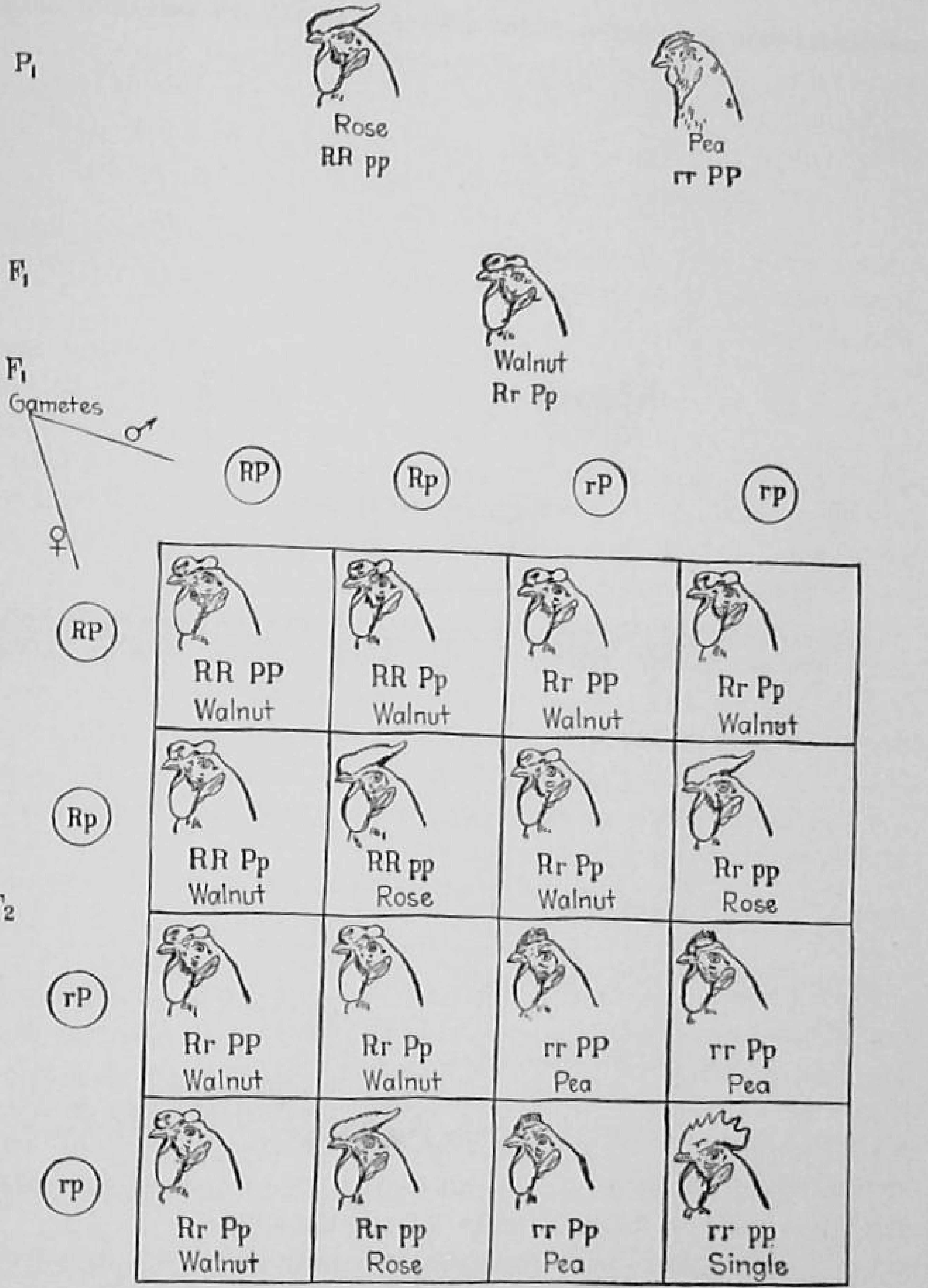

FIG. 91.—Diagram showing interaction of factors for comb form in fowls. The cross of a pure rose-comb bird with a pure pea-comb one gives all walnut-combed offspring. The 16 possible combinations of the F_1 gametes, with their genotypes and the phenotypes resulting from factor interaction, are shown in the F_2 checkerboard. (*From Sinnott and Dunn.*)

results to be expected from crossing the trihybrids secured from mating a

rough, black, short-haired guinea pig = *RR BB SS*

to a

smooth, white, long-haired guinea pig = *rr bb ss*
giving the trihybrid rough, black, short *Rr Bb Ss*

remembering that these trihybrids can secrete the following sorts of germ cells (for these genes are in different chromosomes): *RBS*, *RBs*, *RbS*, *Rbs*, *rBS*, *rBs*, *rbS*, *rbs*.

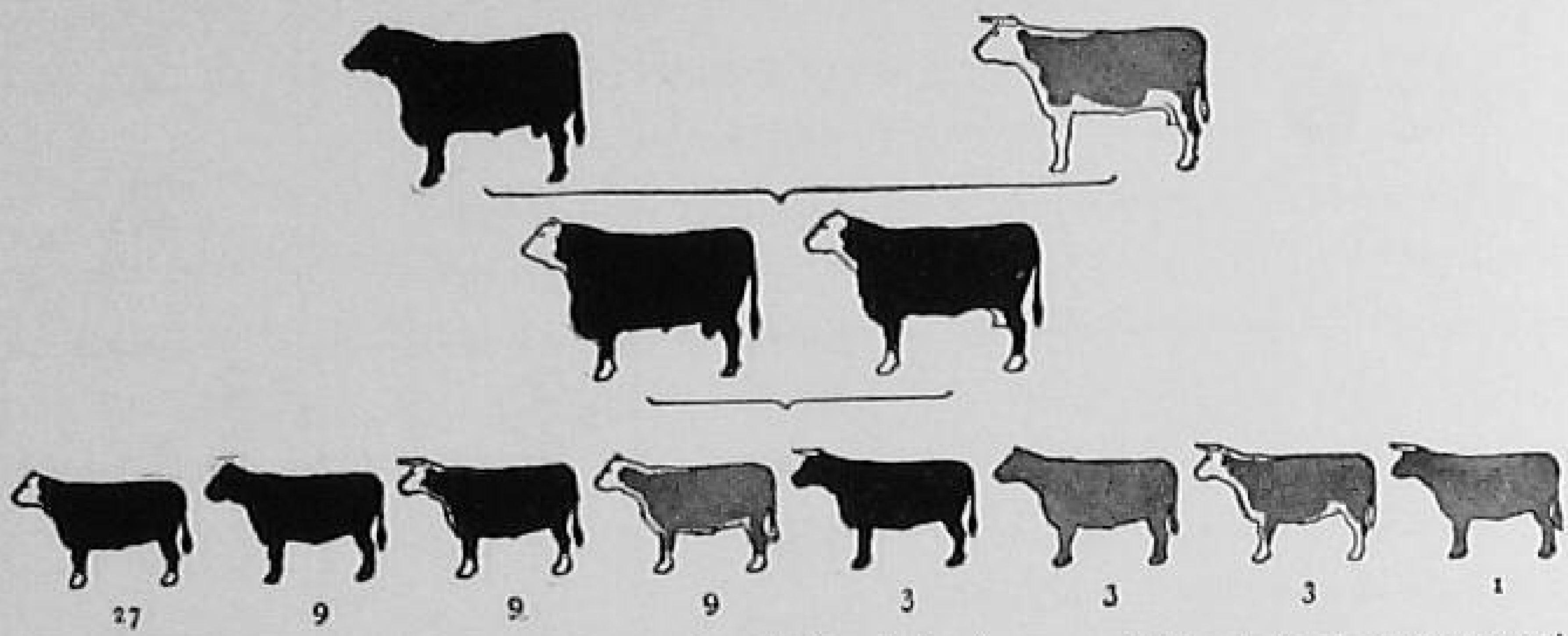

FIG. 92.—Diagram showing inheritance of polled, white face, and black body characteristics and their allelomorphs in an Angus-Hereford cross through F_2.

A similar problem can be worked out in cattle involving the crossing of Angus and Herefords.

Angus (polled,[1] black body, black face) = *PP BB ww*
Hereford (horned, red body, white face) = *pp bb WW*
The monohybrid cross = 3:1 ratio
The dihybrid cross = $(3:1)^2$ ratio, or 9:3:3:1
The trihybrid cross = $(3:1)^3$ ratio, or 27:9:9:9:3:3:3:1

Multifactor Crosses.—Little and Phillips report an experiment involving four pairs of independently Mendelizing factors in mice. They crossed a wild male of the genetic constitution *AA BB DD PP* (*A* for

[1] In crosses between polled and horned breeds of cattle the offspring are not by any means all polled, even though it is true that the latter condition is due to a dominant gene and in spite of the fact that the polled parent is homozygous. Some scurred and horned animals usually appear. This can be explained by postulating a gene for scurs (*Sc*), which is epistatic to polled (*P*) in either heterozygous (*Sc sc*) or homozygous (*Sc Sc*) males, but which is epistatic only in females that are homozygous (*Sc Sc*). A similar epistatic relation apparently holds for a special horn gene (*Ha*), distinct from the gene (*H*), carried by all horned breeds, and found principally in certain horned breeds of Africa. (*Kans. Agr. Expt. Sta. Bien. Rept.* p. 87, 1936.)

agouti pattern, *B* for black coat, *D* for intensity factor, and *P* a factor for eye coloration) on a pink-eyed, dilute, brown female of the genetic constitution *aa bb dd pp*. The observed ratios from such a cross in the F_2 were in all cases very close to expectations. The chromosomal interpretation of the segregation and recombination of factors in this cross is the same as was found in the mono-, di-, and trihybrids.

In the case of a monohybrid, 4 individuals are secured in the F_2 checkerboard; a dihybrid gives 16; a trihybrid, 64. One involving four pairs of contrasted characters would furnish 256 individuals in the F_2; and, if ten characters were considered simultaneously, 1,048,576 individuals would have to be considered in the F_2 generation. It can readily be seen that the problem is becoming unwieldy. For this reason, very few crosses involving as many as four pairs of contrasted characters have been worked out.

Most of the commercially important characters of our farm mammals do not behave in inheritance as though they were determined by only one, two, or three pairs of genes, but rather as though they were determined by the combined interaction of dozens or scores of pairs of genes, probably scattered through all the chromosomes. A different technique must, therefore, be employed when dealing with characters determined by many genes. Even though a character was determined by as few as three genes, we have seen that in the F_2 we could get eight different genotypes.

Ova	Spermatozoa: *PWB*	*PWb*	*PwB*	*Pwb*	*pWB*	*pWb*	*pwB*	*pwb*
PWB	*PP WW BB*	*PP WW Bb*	*PP Ww BB*	*PP Ww Bb*	*Pp WW BB*	*Pp WW Bb*	*Pp Ww BB*	*Pp Ww Bb*
PWb	*PP WW Bb*	*PP WW bb*	*PP Ww Bb*	*PP Ww bb*	*Pp WW Bb*	*Pp WW bb*	*Pp Ww Bb*	*Pp Ww bb*
PwB	*PP Ww BB*	*PP Ww Bb*	*PP ww BB*	*PP ww Bb*	*Pp Ww BB*	*Pp Ww Bb*	*Pp ww BB*	*Pp ww Bb*
Pwb	*PP Ww Bb*	*PP Ww bb*	*PP ww Bb*	*PP ww bb*	*Pp Ww Bb*	*Pp Ww bb*	*Pp ww Bb*	*Pp ww bb*
pWB	*Pp WW BB*	*Pp WW Bb*	*Pp Ww BB*	*Pp Ww Bb*	*pp WW BB*	*pp WW Bb*	*pp Ww BB*	*pp Ww Bb*
pWb	*Pp WW Bb*	*Pp WW bb*	*Pp Ww Bb*	*Pp Ww bb*	*pp WW Bb*	*pp WW bb*	*pp Ww Bb*	*pp Ww bb*
pwB	*Pp Ww BB*	*Pp Ww Bb*	*Pp ww BB*	*Pp ww Bb*	*pp Ww BB*	*pp Ww Bb*	*pp ww BB*	*pp ww Bb*
pwb	*Pp Ww Bb*	*Pp Ww bb*	*Pp ww Bb*	*Pp ww bb*	*pp Ww Bb*	*pp Ww bb*	*pp ww Bb*	*pp ww bb*

FIG. 93.—Checkerboard of F_2 cross between a polled, black-bodied Angus and a horned, white-faced, red-bodied Hereford.

27 with at least one *A*, one *B*, and one *C*.
9 with at least one *A*, one *B*, and *c*'s.
9 with at least one *A*, *b*'s, and one *C*.
9 with *a*'s, one* *B*, and one* *C*.
3 with at least one *A*, *b*'s, and *c*'s.
3 with *a*'s, one* *B*, and *c*'s.
3 with *a*'s, *b*'s, and one* *C*.
1 with *a*'s, *b*'s, and *c*'s.

* At least.

This is a total of 64 individuals in the F_2 and represents 27 different genotypes. Only one of these genotypes (the last one, involving all small letters), can be recognized on sight, so that breeding tests would have to be instituted to reveal the genotypic differences between *AA BB CC* and *Aa BB Cc* individuals, etc. So the fact that there apparently are so few unit characters (determined by one or a few pairs of genes only) in our farm animals is no great loss or hardship, for it is not practical to deal with more than one or two pairs of genes at a time, especially in species which have relatively as few offspring as our farm animals and where the

TABLE 19.—RELATION BETWEEN THE NUMBER OF GENE PAIRS INVOLVED IN A CROSS AND THE NUMBER OF PHENOTYPIC AND GENOTYPIC CLASSES IN THE F_2

Number of gene pairs involved	Number of visibly different F_2 classes if dominance is complete	Number of different kinds of gametes formed by F_1	Number of genotypically different combinations	Number of possible combinations of F_1 gametes
1	2	2	3	4
2	4	4	9	16
3	8	8	27	64
4	16	16	81	256
n	2^n	2^n	3^n	4^n

proper combinations of several genes might by chance never be secured in the small numbers available.

The above table should help to make this point clear.

It must be remembered that, in order to secure independent segregation in all the types of hybrids studied above, it is necessary that the genes be located in different chromosomes. This of necessity limits, in any species, the number of pairs of contrasted characters that can show independent assortment to the number of pairs of chromosomes found in that species. *Drosophila melanogaster*, for example, with four pairs of chromosomes could not manifest more than four pairs of independently segregating characters at any one time. No cases have been discovered where there are more independently segregating pairs of contrasted characters than there are pairs of chromosomes. If, in Drosophila, five pairs of contrasted characters were considered at one time, it would, of necessity, mean that at least two of these pairs of characters were determined by factors carried in the same chromosome. Such a condition is known as *linkage* and will be discussed later.

MODIFIED TWO-GENE RATIOS—DOMINANCE LACKING

We have seen above that, if two genes which determine different characters are located in different chromosomes and one of the members of

each pair of genes is dominant over its allele, we will secure a 9:3:3:1 ratio when we cross two F_1 dihybrids to get the F_2 generation, and that the same ratio holds if the two genes control only one character (comb pattern in poultry).

However, if one pair of genes lacks dominance, we would not get a 9:3:3:1 but a 3:6:3:1:2:1 ratio, because the first phenotype containing 9 individuals breaks up into phenotypes containing 3 and 6 individuals each; whereas the third phenotype containing 3 individuals breaks up into two phenotypes containing 1 and 2 individuals each. The following figure will be useful in explaining all of the various modifications of the 9:3:3:1 ratio.

Aa Bb × *Aa Bb*

Eggs	Sperm			
	AB	*Ab*	*aB*	*ab*
AB	*AA BB*(1)	*AA Bb*(5)	*Aa BB*(9)	*Aa Bb*(13)
Ab	*AA Bb*(2)	*AA bb*(6)	*Aa Bb*(10)	*Aa bb*(14)
aB	*Aa BB*(3)	*Aa Bb*(7)	*aa BB*(11)	*aa Bb*(15)
ab	*Aa Bb*(4)	*Aa bb*(8)	*aa Bb*(12)	*aa bb*(16)

FIG. 94.—Generalized checkerboard of a two-gene cross.

If we crossed a polled,[1] red animal, *AA BB*, with a horned, white one, *aa bb*, the F_1 would be polled and roan,[2] *Aa Bb*, assuming gene *A* for polled to be dominant over gene *a* for horns, but gene *B* for red not to be dominant over gene *b* for white, the presence of both *B* and *b* giving the roan color. Then we would have in Fig. 94:

Squares (1), (3), and (9)........................ 3 polled, red
Squares (2), (4), (5), (7), (10), and (13)........... 6 polled, roan
Squares (6), (8), and (14)........................ 3 polled, white
Square (11).................................... 1 horned, red
Squares (12) and (15)........................... 2 horned, roan
Square (16).................................... 1 horned, white

If dominance were lacking in both pairs of genes, as it is in a cross between a red-flowered broad-leaved (*AA BB*) and a white-flowered narrow-leaved (*aa bb*) snapdragon, for the F_1 is pink-flowered with leaves of intermediate width, then the F_2 would comprise *AA* red, *Aa* pink,

[1] We are departing from our usual notation in order to be able to use one figure of reference for all the types of variation due to lack of dominance and epistasis.

[2] Dominance between red and white color lacking.

aa white, *BB* broad, *Bb* intermediate, *bb* narrow (see Fig. 94), and we would have in the F_2

1 red, broad (square 1)
2 pink, broad (squares 3 and 9)
2 red, intermediate (squares 2 and 5)
4 pink, intermediate (squares 4, 7, 10, 13)
1 red, narrow (square 6)
2 pink, narrow (squares 8 and 14)
1 white, broad (square 11)
2 white, intermediate (squares 12, 15)
1 white, narrow (square 16)

or a 1:2:2:4:1:2:1:2:1 ratio.

Breeding results with both plants and animals have revealed several characters that behave in inheritance as though they were controlled by two pairs of genes but do not follow the usual pattern as evidenced in comb type in poultry described earlier in this chapter where the mating of rose-combed birds (*RR pp*) with pea-combed birds (*rr PP*) gave an F_1 of all walnut combs (*Rr Pp*) and an F_2 of 9 walnuts, 3 rose, 3 pea, and 1 single comb. In order to explain these deviating results, the principle of epistasis has been invoked. Again the student is reminded that the *modus operandi* of genetics is to get the results first by breeding plants and animals, and, after the results are secured, to devise a theory which will provide a rational and logical interpretation for the breeding results.

Epistasis is the same relation between pairs of different genes that dominance is between different single genes of one pair of alleles, *i.e.*, gene *A* may be dominant over its allele *a*, or, in an epistatic sense, gene *A* may be dominant over genes *B* or *b* (dominant epistasis), or genes *aa* may be dominant over genes *B* or *b* (recessive epistasis), or both these conditions may hold at the same time, dominant and recessive epistasis. We may further find cases where duplicate dominant, duplicate recessive, or incompletely duplicate epistasis may prevail.

We will presently describe six relatively simple forms of epistatic behavior. The student should realize, however, that there is an almost limitless number of possible interactions between two, three, or more pairs of the several thousand genes which are the hereditary capital of our farm animals. Careful studies by a host of experimenters have delineated the broad, general principles of inheritance. One of these general principles is called *epistasis*, but the number of possible epistatic effects is legion.

Some would even go so far as to call all nonadditive factor interaction epistatic.

Recessive Epistasis.—If we mate a black rat, *AA BB* (gene *A* for color, genes *aa* diluted color, gene *B* for expression of any color, genes *bb* masking all color, *i.e.*, epistatic to *A*) to an albino rat, *aa bb*, all of the F_1 are black, *Aa Bb*, whereas the F_2 will appear as 9 blacks, 3 creams, and 4 whites. This is due to the fact that the presence of at least one *A* and one *B* produces black (squares 1, 2, 3, 4, 5, 7, 9, 10, and 13, Fig. 94), *a*'s and at least one *B* produce cream (squares 11, 12, and 15, Fig. 94), whereas either *AA*, *Aa*, or *aa*, together with *b*'s (squares 6, 8, 14, and 16, Fig. 94), produce albino. This is because the *b*'s mask the expression of *A* or *a*; *i.e.*, *b* is epistatic to *A* or *a*, so that two portions of the usual 9:3:3:1 ratio are thrown together phenotypically.

Incompletely Duplicate Epistasis.—Another manifestation of epistasis is one that throws the two middle portions of the 9:3:3:1 ratio together phenotypically. An example of this occurs in Duroc-Jersey swine, where one sandy-colored race is *AA bb* and another *aa BB*. When crossed the F_1 are all red, *Aa Bb*, and in the F_2 all the offspring, which get at least one *A* and one *B* (squares 1, 2, 3, 4, 5, 7, 9, 10, and 13, Fig. 94), are red, those getting neither *A* nor *B* (square 16) are white, and all the others, getting at least one *A* with *b*'s or at least one *B* with *a*'s, are sandy (squares 11, 12, 15, 6, 8, and 14, Fig. 94). These are sometimes called *mutually supplementary genes*. A similar case in plants has been found in the fruit shape of squash, where genes *A* and *B* together give disk shape, genes *AA* or *Aa* with *bb* and genes *aa* with *BB* or *Bb* give spherical shape, and the double recessive genes give elongated shape.

Dominant Epistasis.—It has been found that a certain type of white dogs, *AA BB* (with color in the eyes), if mated to brown dogs, *aa bb*, produce all white offspring, and that, when these F_1 are mated, the peculiar ratio of 12:3:1 appears in F_2. This apparently is due to the white dog carrying color factors (*A*) that are inhibited from forming color in the hair by another gene (*B*). The brown dogs lack the gene for black color *A*, being therefore brown in color, for they also lack the inhibitor *B*. The F_1 cross is *Aa Bb* and is white because of the dominant epistatic effect of gene *B* over gene *A* or *a*, whereas in the F_2 all those squares that get at least one *B* (1, 2, 3, 4, 5, 7, 9, 10, 11, 12, 13, and 15, Fig. 94), are white, those getting *b*'s and at least one *A* (squares 6, 8, and 14, Fig. 94) being black, and the remaining (square 16), *aa bb*, being brown. Genes that behave in this fashion are often called *inhibitors*.

Other Types of Epistasis.—Further types of epistasis that the student can work out by means of Fig. 94 are:

Duplicate Recessive Epistasis. *aa* epistatic to *BB*, *Bb*, or *bb*.
bb epistatic to *AA*, *Aa*, or *aa*.

Sweet peas: white pea *AA bb* × white pea *aa BB*.
F_1 *Aa Bb*, all purple.
F_2 9 purple: 7 white.

Homo sapiens: deaf person *AA bb* × deaf person *aa BB*.
F_1 *Aa Bb*, all normal hearing.
F_2 9 normal hearing: 7 deaf.

Duplicate Dominant Epistasis. *A* epistatic to *BB*, *Bb*, or *bb*.
B epistatic to *AA*, *Aa* or *aa*.

Poultry: feathered shanks *AA BB* × clean shanks *aa bb*.
F_1 *Aa Bb*, all feathered shanks.
F_2 15 feathered shanks: 1 clean shanks.

Shepherd's-purse (Bursa): triangular seed pod *AA BB* × top-shaped seed pod *aa bb*.
F_1 *Aa Bb*, all triangular seed pods.
F_2 15 triangular seed pod: 1 top-shaped seed pod

Dominant and Recessive Epistasis. *aa* epistatic to *BB*, *Bb*, or *bb*.
B epistatic to *AA*, *Aa*, or *aa*.

Poultry: White Leghorn *AA BB* × White Wyandotte *aa bb*.
F_1 *Aa Bb*, all white.
F_2 13 white: 3 colored birds.

Summary on Epistasis.—We have seen from the above examples that the usual two-gene phenotypic ratio of 9:3:3:1 may be modified in a variety of ways by dominance between individual genes in an allelic pair and by various epistatic manifestations between pairs of genes.

The following diagram brings all the above facts into one complete whole.

The complications introduced into breeding practice are illustrated in the following figure. In column I, we see that all the 9 genotypes found in an F_2 of a cross involving two pairs of genes stand out clearly from each other (*AA BB*, *AA Bb*, *AA bb*, *Aa BB*, *Aa Bb*, *Aa*, *bb*, *aa BB*, *aa Bb*, and *aa bb*). Because dominance is lacking, *AA*, *Aa*, and *aa* combinations are different, and the same is true of *BB*, *Bb*, and *bb* combinations. In other words, the phenotypes and the genotypes are the same, or the breeder knows the genotype when he sees the phenotype. Dominance makes its appearance in one pair of genes (*A*) in column II with the result that *AA BB* and *Aa BB* can no longer be separated by phenotypic inspection but must be subjected to breeding trials to ascertain their genetic make-up. Similarly, *AA Bb* and *Aa Bb* are now indistinguishable phenotypically, etc. The 9 genotypes of column I have been reduced to 6 phenotypes in column II and are further reduced to 4 in column III. Likewise further

reduction of the 9 original phenotypes of column I to various combinations of 3 and 2 genotypes in columns IV to IX are indicated. Dominance and epistasis complicate breeding practice, because they hide two or several genotypes in one phenotype.

It should be remembered also that we are here dealing with a comparatively simple thing, because it involves only two pairs of genes. If three pairs of genes were acting on the same character and there was no dominance, we would get a phenotypic ratio of 27:9:9:9:3:3:3:1 in the F_2. It is not difficult to imagine the complications that dominance and epistasis would introduce into this situation, and it appears likely that the

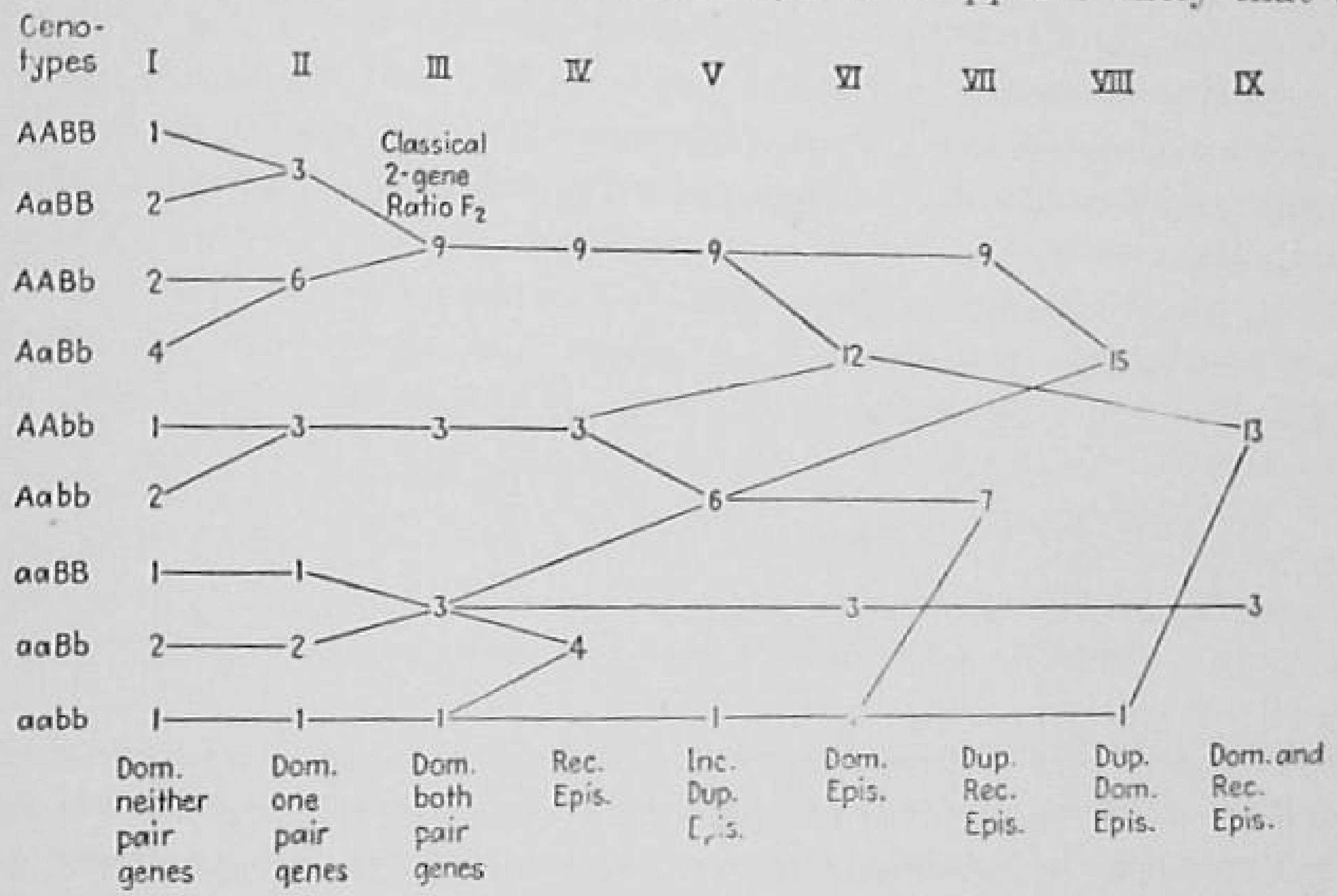

FIG. 95.—Phenotypic classes in two-gene F_2, due to dominance and epistasis.

commercially valuable characters of our larger farm animals were influenced by dozens or hundreds of genes.

Two things are apparent: (1) the scientific livestock breeders need a thorough knowledge of the basic principles of hereditary transmission as worked out with small laboratory animals; and (2) the breeder of the larger animals finds little opportunity to apply this detailed knowledge to his own immediate problems but is forced to devise his own methods of selection and improvement on the basis of the broad principles that have been ascertained through the breeding of laboratory animals.

Analysis of Coat Color in Mice.[1]

A thorough study of the variations in a group of related characters in any organism will usually reveal an intricate series of interactions between the com-

[1] SINNOTT, EDMUND W., DUNN, L. C., and DOBZHANSKY, TH., "Principles of Genetics," 4th ed., pp. 111–115, McGraw-Hill Book Company, Inc., New York, 1950.

ponent genes. As an example we shall choose the house mouse, for in this animal a large number of spontaneous variations have provided the opportunity for a genetic analysis of the genes affecting coat color. Many such genes have been studied and their interrelationships made out. *C* is the fundamental color gene, necessary, for the production of any pigment in the coat. Another gene, *A* or gray, determines the development of the agouti pattern. Its recessive allele, *a* is present in the nonagouti mice, such as blacks or browns. Still another, *B*, governs the development of black pigment and is dominant over its allelic condition of brown or chocolate, *b*. Many varieties are spotted with white in a blotched or piebald pattern, and such mice contain a gene, *s*, which is recessive to self or solid color, *S*. Another gene, *d*, brings about a clumping of the black and brown pigment granules in the hairs and makes these colors appear faded or dilute, as opposed to the normal fully pigmented form, *D*. Another gene reduces the amount of black and brown pigment in the fur, giving it a pale and washed-out appearance, and also reduces the pigment in the iris, making the eyes appear reddish or pink like the eyes of albinos. The gene, which is called pink eye (*p*) from its most noticeable effect, is recessive to the normal dark-eyed intense-colored condition, *P*. These genes all segregate sharply and may occur in any combination. There are also several other genes affecting coat color which will be omitted for the sake of simplicity. Some of these combinations result in characters which are distinctive and have been given names of their own. Thus the nonblack agoutis are called "cinnamon" or brown agouti; the dilute blacks, "blue"; the dilute browns, "silver fawn"; and so on. Table 20 lists these various gene combinations, together with the type of coat color produced by each.

All of these types are recessive to the wild coat and appear to have arisen from it by mutation of one or more genes. Thus at any time the wild type may be reconstituted by bringing into combination all of the alleles of the genes which are responsible for these new types. In fact, the wild coat color itself is found to depend on the presence and interaction of all of the genes named. Thus, in order to produce the agouti pattern, there must be present the genes for color (*C*), agouti (*A*), black (*B*), dark eye (*P*), dense color (*D*), and solid color (*S*). With regard only to these genes the genotype of the wild mouse may be written *AA BB CC DD PP SS*. These genes all show essentially complete dominance, so that their heterozygous condition will give the same result as is produced by the homozygous form here given. Thus an animal with the genotype *Aa Bb Cc Dd Pp Ss* would also be agouti in appearance. The genes named do not include all that are known, nor is it believable that more than a small sample of the genes affecting coat color in mice have been studied. Were knowledge complete, it is probable that the list of genes necessary for the production of the agouti pattern would be much longer and that the letters of the alphabet would be exhausted in attempting to write the genotype of the wild mouse. Here, then, is a clear and convincing example of gene interaction. In order that the apparently simple pattern characteristic of wild house mice may be developed, there must be present at least six genes (probably many more) each of which has

TABLE 20.—INTERACTION OF GENES FOR COAT COLOR IN MICE

Genes						Gametic formula	Phenotype
C	*A*	*B*	*D*	*P*	*S*	*CABDPS*	Wild-type agouti
C	*A*	*B*	*D*	*P*	*s*	*CABDPs*	Spotted agouti
C	*A*	*B*	*D*	*p*	*S*	*CABDpS*	Pink-eyed agouti
C	*A*	*B*	*D*	*p*	*s*	*CABDps*	Pink-eyed, spotted agouti
C	*A*	*B*	*d*	*P*	*S*	*CABdPS*	Dilute agouti
C	*A*	*B*	*d*	*P*	*s*	*CABdPs*	Spotted, dilute agouti
C	*A*	*B*	*d*	*p*	*S*	*CABdpS*	Pink-eyed, dilute agouti
C	*A*	*B*	*d*	*p*	*s*	*CABdps*	Pink-eyed, spotted, dilute agouti
C	*A*	*b*	*D*	*P*	*S*	*CAbDPS*	Cinnamon
C	*A*	*b*	*D*	*P*	*s*	*CAbDPs*	Spotted cinnamon
C	*A*	*b*	*D*	*p*	*S*	*CAbDpS*	Pink-eyed cinnamon
C	*A*	*b*	*D*	*p*	*s*	*CAbDps*	Pink-eyed, spotted cinnamon
C	*A*	*b*	*d*	*P*	*S*	*CAbdPS*	Dilute cinnamon
C	*A*	*b*	*d*	*P*	*s*	*CAbdPs*	Spotted, dilute cinnamon
C	*A*	*b*	*d*	*p*	*S*	*CAbdpS*	Pink-eyed, dilute cinnamon
C	*A*	*b*	*d*	*p*	*s*	*CAbdps*	Pink-eyed, spotted, dilute cinnamon
C	*a*	*B*	*D*	*P*	*S*	*CaBDPS*	Black
C	*a*	*B*	*D*	*P*	*s*	*CaBDPs*	Spotted black
C	*a*	*B*	*D*	*p*	*S*	*CaBDpS*	Pink-eyed black
C	*a*	*B*	*D*	*p*	*s*	*CaBDps*	Pink-eyed, spotted black
C	*a*	*B*	*d*	*P*	*S*	*CaBdPS*	Dilute black
C	*a*	*B*	*d*	*P*	*s*	*CaBdPs*	Spotted, dilute black
C	*a*	*B*	*d*	*p*	*S*	*CaBdpS*	Pink-eyed, dilute black
C	*a*	*B*	*d*	*p*	*s*	*CaBdps*	Pink-eyed, spotted, dilute black
C	*a*	*b*	*D*	*P*	*S*	*CabDPS*	Brown
C	*a*	*b*	*D*	*P*	*s*	*CabDPs*	Spotted brown
C	*a*	*b*	*D*	*p*	*S*	*CabDpS*	Pink-eyed brown
C	*a*	*b*	*D*	*p*	*s*	*CabDps*	Pink-eyed, spotted brown
C	*a*	*b*	*d*	*P*	*S*	*CabdPS*	Dilute brown
C	*a*	*b*	*d*	*P*	*s*	*CabdPs*	Spotted, dilute brown
C	*a*	*b*	*d*	*p*	*S*	*CabdpS*	Pink-eyed, dilute brown
C	*a*	*b*	*d*	*p*	*s*	*Cabdps*	Pink-eyed, spotted, dilute brown
c	with any other genes					*c*	Albino, may be of any of 32 genotypes above

a definite effect on coat color. If any single gene is missing or changed, a coat pattern differing more or less widely from the wild type results.

This type of gene interaction is not exceptional but is found whenever numerous variations in a single aspect of the organism are carefully analyzed. Such analyses have been made for several groups of characters in maize. More than a dozen series of genes affecting chlorophyll development in this plant are known. The normal color is green, which results from the combined action of all of the normal genes. If one of these genes such as W mutates to a recessive allele w, the seedling is albinotic, virtually without any chlorophyll, and being unable to carry on photosynthesis it soon dies. There are at least 15 different genes susceptible to this type of change, which means that there are at least 15 genetically different types of albinos. In another group of recessive mutants known as lutescents only yellow pigment develops; in another group are more than 20 recessive genes each of which when homozygous produces virescent seedlings which are albinotic but eventually develop enough chlorophyll to keep them alive. Other recessive genes are responsible for pale green color (10 known), zebra-striping (4 known), piebald spotting (4 known), golden color (4 known), yellow-green color (3 known), yellow striping (2 known), fine white striping (3 known), and many other modifications of chlorophyll composition and arrangement. It must be true therefore that the normal development of chlorophyll in maize depends on interaction among at least 75 different genes. If any one of these changes by mutation from the normal to the recessive allele, some essential step in the interaction fails and the chlorophyll is absent or deficient in some way. Similarly each of another large group of genes conditions some step in the development of anthocyanin pigments, while the normal starchy endosperm of the kernel of field corn (dent or flint) depends on the interaction of more than 30 different genes. The results of the analysis of such cases as those described above suggest that many of the characters of organisms are the end products of long chainlike series of related steps, $a \rightarrow b \rightarrow c \rightarrow d \rightarrow n$. Separate genes seem to affect separate steps so that if the gene affecting step b does not perform its task, then c and all later steps which depend upon it cannot take place and the character, such as normal chlorophyll, cannot appear. Other evidence for this view of the mechanism of gene interaction will be presented in a later chapter. Whatever the means by which the genes interact, it may be accepted as a general rule that the hereditary characters of a plant or animal depend upon the balanced cooperation of a large number of genes.

Ibsen has made an extended study of the inheritance of coat colors in cattle.[1] It was found necessary to postulate about 25 genes to account for the now known color patterns in our domestic cattle. This example serves to show the extreme complexity of the problem of inheritance in our larger animals. It is undoubtedly even more complex in regard to their commercially valuable qualities. Who would dare even to guess

[1] IBSEN, A. H. L., Cattle Inheritance (Color), *Genetics*, **18**:441–480, September, 1933.

how many genes may be involved in the final expression of the amount of milk a cow may yield to say nothing of the environmental influences involved in such a matter? We can be fairly sure of the fact that many, many genes are involved in determining the characteristics of our livestock, and we can be very sure that they behave in ways comparable to those used as illustrations of different types of inheritance in this and the following few chapters of this book. It may be that we will never know the exact number and interrelations of the genes involved in milk production. Nevertheless, it should be possible to improve our breeding practices on the basis of the general principles involved in the hereditary transmission of characteristics.

Aspects of Dominance.—In the early part of the twentieth century, soon after the rediscovery of Mendel's laws of inheritance, there was a tendency toward oversimplification of the theory. That is to say, there was a tendency to think of each potentiality as determined by one gene only. We are now aware of the fact that, rather than one gene's determining a potentiality, many or all the genes (together with the environment) interact to bring the potentiality to full fruition, though, of course, one gene may still determine the appearance or nonappearance of a definite potentiality.

In like manner the idea of dominance held full sway in the early days of genetics. We now recognize that dominance is a relative rather than an absolute term. For example, brown eyes in man are dominant over blue, but the blue-eyed condition is in turn dominant over red or pink eyes (albinism). Whether blue eyes are dominant or recessive depends therefore on what the characteristic is to which they are being contrasted. There are varying degrees of dominance, from complete dominance to an entire lack of dominance. The possibility also exists that the phenomenon of "overdominance" in which the heterozygote is superior to either homozygote may occur.

The results from crossing tall and dwarf peas; smooth, black and rough, white guinea pigs; or polled, black-bodied black-faced and horned, red-bodied white-faced cattle were clear-cut because in every instance one character was wholly dominant over its allele. If, however, a cross is made between a red Shorthorn and a white one, the result is a roan (mixture of red and white hairs) color pattern. Likewise a cross between a black fowl and a white one gives the typical Blue Andalusian pattern, and a cross between red- and white-flowered four-o'clocks gives a pink hybrid. In these cases, dominance is lacking, and hybrids of this sort never breed true to their own phenotypic appearance because their phenotypic character is due to the interaction of two genes, whereas they can transmit only one gene or the other to any one offspring.

The hybrid character is different from either of the parents; *i.e.*, red crossed with white Shorthorn yields roan, and apparently the final expression of this characteristic hinges on one pair of genes. Similarly in poultry, pea-shaped comb and rose-shaped comb are each individually dominant over a single comb, whereas a cross between homozygous rose- and pea-combed birds yields a new comb character, *viz.*, walnut. To explain these facts two sets of alleles must be postulated and the genetic constitution of a single-combed bird becomes *rr pp*, whereas a pure rose is *RR pp* and a pure pea *rr PP*. These genes (*R* and *P*) are evidently located on different chromosomes, are therefore inherited separately, or according to the law of independent assortment, but act together in producing the final expression of the comb characteristic. If we cross pea-combed and rose-combed birds, the F_1 will all be walnut-combed and the F_2 will give the usual 9:3:3:1 hybrid ratio, (walnut, rose, pea, single).

Dominance may at times be quite variable, depending upon the presence or absence of certain supplementary genes, and, finally, a characteristic may act as a dominant in one sex (baldness in man) and as a recessive in the other. It is seen, therefore, that the idea of dominance is not the simple thing it was at one time supposed to be.

Occurrences such as the roan pattern in Shorthorn cattle was formerly often spoken of as *blending inheritance*, though the term went out of use as the discrete, atomic nature of the genes became probable. The fact that, when large races of animals are crossed with small ones, offspring result which are intermediate in size induces some still to speak of these offspring as being a *blend* of the two parent races. In terms of chromosomes and genes, of course, they are, but it is now fairly apparent that most of the commercially valuable characters of our animals are determined by the interaction of scores or hundreds of genes rather than by one or two pairs. In this sense, such crossing does result from a blending of many genes, although the genes themselves remain discrete bodies. It is fortunate that inheritance is not blending in nature, for if each individual were an average of its two parents, the entire population would be almost completely uniform in a few generations. Dominance generally behaves in the same manner in closely related species, and in most mammals the albino (recessive) gene is the same. However, a characteristic that is dominant in one species may be recessive in another, *e.g.*, black is dominant over white in guinea pigs, but in farm pigs we have learned by experience that white is dominant over black. The expression of dominance may also be influenced by the environment, age, sex, and by other genes in the organism. In short, dominance is variable with many gradations.

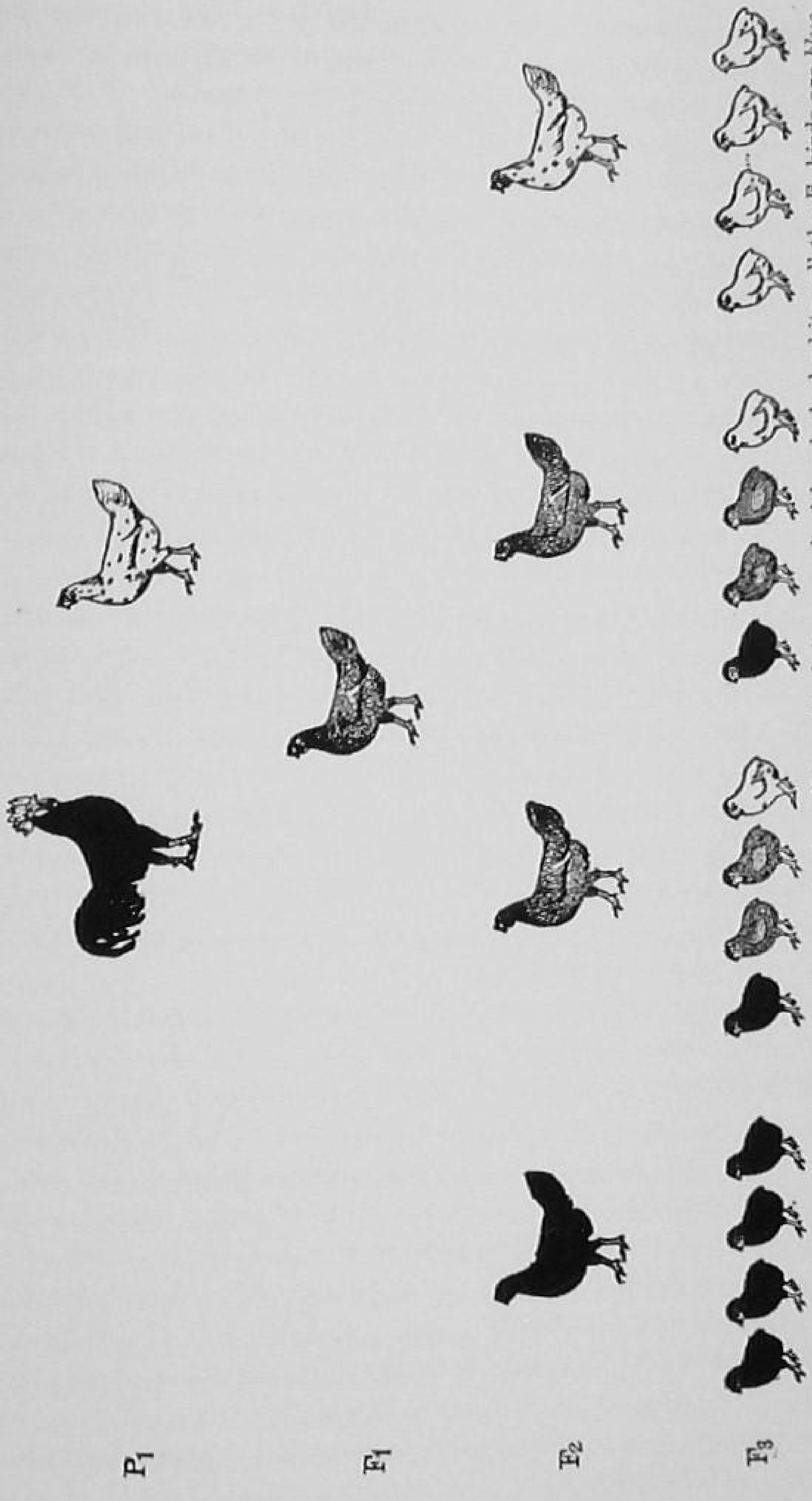

FIG. 96.—The inheritance of blue in Andalusian fowls. When black is crossed with splashed white, all the F_1 birds are *blue*. These, if bred together, produce ¼ black, which breed true; ½ blue which breed like the F_1 blue; and ¼ white, which breed true.

The nature of the recessive condition has also been a much-debated question. Some authorities claimed that the recessive gene was a definite entity, others that the recessives indicated losses of genes. T. H. Morgan has adduced evidence from several sources which indicates that recessives are not due to losses of genes; *e.g.*, the fact that albino rats always have a few colored hairs on the feet, that the wings of fruit flies attain considerable length if the temperature is held at 31°C. even though the flies be genetically pure recessive vestigials, and that small eyes appear in old cultures of Drosophila that are pure eyeless recessives. He also cites the fact that certain recessive mutations have been known to revert to the original dominant condition and finally that there are more than a dozen known mutants of eye color in Drosophila at the same locus. From this evidence, it would seem that recessives are caused by the action of definite entities (genes) just as are dominant characteristics and that the idea of considering recessives as losses of genes is an untenable one.

The student should try to appreciate fully that the facts of breeding came first, theories to explain them second. Genetics is but a systematic arrangement of breeding facts together with theories that offer a logical explanation. Any theory must do two things: (1) explain past facts and (2) allow us to prognosticate. All the theories of genetics to be discussed later are backed by a multitude of fact. As soon as a new fact is discovered which cannot be fitted into the presently accepted theory, that theory will have to be supplanted by one which will accommodate all the old plus the new facts. This revision of theory has been necessary many times in the past short life of genetics.

Summary.—In this chapter we have become acquainted with some of the simpler but basic principles of heredity. We have learned that heredity is referable to paired, particulate bodies called *genes*, located in the chromosomes. We have seen that these genes retain their identity at all times whether expressed phenotypically or not. We are now familiar with two of the basic laws of heredity, *viz.*, segregation and independent assortment of the chromosomes. The latter exist in pairs, and one complete set (haploid, n) is given to each offspring by each of its parents through an egg or a sperm, which makes each offspring diploid or $2n$. This offspring in turn passes on a random sample of its chromosomes, one of each pair, however, to each of its offspring. We traced this procedure where one, two, or three pairs of genes in separate chromosomes were involved. We learned the F_2 monohybrid ratio to be 3:1 phenotypically (or 1:2:1 genotypically) and the F_2 dihybrid ratio to be 9:3:3:1 phenotypically. Finally, we studied various modifications of the two-gene ratio due to lack of dominance between alleles or between pairs of

genes, the latter condition being known as *epistasis*, and attempted to clarify our minds regarding several aspects of dominance and recessiveness.

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Problems[1]

The following problems are designed to promote facility in correct genetic thinking. Not until you can work these and similar problems quickly and correctly will you have a comprehensive grasp of the genetic principles that they illustrate.

1. If a homozygous rough-coated animal is crossed with a smooth one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 back on its rough parent? On its smooth parent?

2. A certain rough-coated guinea pig bred to a smooth one gives 8 rough and 7 smooth offspring. What are the genotypes of parents and offspring?

3. If one of the rough F_1 animals in the preceding question is mated to its rough parent, what offspring may be expected?

4. Two rough-coated guinea pigs when bred together produce 18 rough and 1 smooth offspring. What are the genotypes of the parents?

5. Cross a homozygous rough, black animal with a smooth, white one. What will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 black with the rough, black parent? With the smooth, white one?

6. In the F_2 generation in the preceding question, what proportion of the rough, black individuals may be expected to be homozygous for both characters?

7. NOTE.—Polled or hornless condition in cattle (P) is dominant over horned (p).

A certain polled bull is bred to three cows. With cow A, which is horned, a horned calf is produced; with cow B, also horned, a polled calf is produced; and with cow C, which is polled, a horned calf is produced. What are the genotypes of all these four animals and what offspring would you expect from these three matings?

8. NOTE.—In Shorthorn cattle the heterozygous condition of red coat color (R) and white (r) is roan.

If two roan Shorthorn cattle are mated, what chance will their offspring have of resembling their parents in coat color?

9. Two black female mice are crossed with a brown male. In several litters female No. 1 produced 9 blacks and 7 browns; female No. 2 produced 17 blacks. What deductions can you make concerning inheritance of black and brown coat color in mice? What are the genotypes of the parents in this case?

10. A breeder has a group of animals all of which are heterozygous for a given dominant character, A, and thus have the genotype Aa. He wants to establish a

[1] These problems and those at the ends of the next two chapters are taken for the most part from lists in Sinnott and Dunn, "Principles of Genetics," 3d ed., McGraw-Hill Book Company, Inc., New York, 1939, and are reproduced here through the kind permission of the authors.

race homozygous for A. To accomplish this he allows these animals to interbreed freely and then practices mass selection among their offspring, saving for breeding all individuals that show the character A and discarding only the aa animals. Members of one generation do not cross with any other. In the third generation, what proportion of the animals which have the character A will be homozygous for it? How could the breeder have established a homozygous strain more easily?

11. If the breeder mentioned in the previous question is practicing mass selection for two characters, A and B, and his original animals have the genotpye $Aa\ Bb$, would selection be effective more rapidly or more slowly than when only one character was concerned? Explain.

12. It has long been known that Blue Andalusian fowls do not breed true to the blue color of their plumage. How do you explain this?

13. What offspring will a Blue Andalusian fowl have if bred to birds of the following plumage colors: (1) black, (2) blue, (3) white?

14. Note.—In man, brown eyes (B) are dominant over blue (b). A brown-eyed man marries a blue-eyed woman and they have 8 children, all brown-eyed. What are the genotypes of all the individuals in the family?

15. A blue-eyed man both of whose parents were brown-eyed marries a brown-eyed woman whose father was brown-eyed and whose mother was blue-eyed. They have one child, who is blue-eyed. What are the genotypes of all the individuals mentioned?

16. Assume that in man, right-handedness (R) is dominant over left-handedness (r). A right-handed man whose mother was left-handed marries a right-handed woman who has three brothers and sisters, two of whom are left-handed. What chance will the children of this marriage have of being left-handed?

17. What are the chances that the first child from a marriage of two heterozygous brown-eyed parents will be blue-eyed? If the first child is brown-eyed, what are the chances that the second child will be blue-eyed?

18. At the time of synapsis preceding the reduction division, the homologous chromosomes align themselves in pairs and one member of each pair passes to each of the daughter nuclei. Assume that in an animal with four pairs of chromosomes, chromosomes A, B, C, and D have come from the father and A', B', C', and D' have come from the mother. In what proportion of the germ cells of this animal will all of the maternal chromosomes be present together? All of the paternal?

19. If one individual is homozygous for four dominant factors and another for their four recessive allelomorphs, and if these two individuals are crossed, what proportion of the F_2 from this cross will resemble each parent, respectively, in appearance?

20. A rough, black guinea pig bred with a rough, white one gives 28 rough, black; 31 rough, white; 11 smooth, black; and 9 smooth, white. What are the genotypes of the parents?

21. Two rough, black guinea pigs when bred together have 2 offspring, one of them rough, white and the other smooth, black. If these same parents were to be bred together further, what offspring would you expect from them?

22. If a homozygous polled, white animal is bred to a horned, red one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 back with the polled, white parent?

23. A polled, roan bull bred to a horned, white cow produces a horned, roan daughter. If this daughter is bred back to her father, what offspring may be expected as to horns and coat color?

24. In swine, white coat is dominant over black and the "mule-footed" condition over that with normal feet. A white, mule-footed boar, A, always produces white, mule-footed offspring, no matter to what sow he is bred. Another boar, B, however, also white and mule-footed, when bred to black sows produces about ½ white and ½ black offspring, and when bred to normal-footed sows, about ½ mule-footed and ½ normal offspring. Explain this difference between these two animals by comparing their genotypes for these two traits.

25. In poultry, feathered legs (*F*) are dominant over clean legs (*f*); and pea comb (*P*) over single comb (*p*).

Two cocks, A and B, are bred to two hens, C and D. All four birds are feathered-legged and pea-combed. Cock A with both hens produces offspring that are all feathered and pea. Cock B with hen C produces both feathered and clean, but all pea-combed, but with hen D produces all feathered but part pea-combed and part single. What are the genotypes of these four birds?

26. In poultry, the factors for rose comb (*R*) and pea comb (*P*), if present together, produce walnut comb. The recessive allelomorphs of both, when present together in a homozygous condition, produce single comb.

What will be the comb character of the offspring of the following crosses, in which the genotypes of the parents are given?

$Rr\,Pp \times Rr\,Pp$	$Rr\,Pp \times Rr\,pp$
$RR\,Pp \times rr\,Pp$	$Rr\,pp \times rr\,Pp$
$rr\,PP \times Rr\,Pp$	$Rr\,pp \times Rr\,pp$

27. In the following five questions, all of which concern comb form in poultry, determine the genotypes of the parents:

A rose crossed with a walnut produces offspring ⅜ of which are walnut, ⅜ rose, ⅛ pea, and ⅛ single.

28. A walnut crossed with a single produces offspring ¼ of which are walnut, ¼ rose, ¼ pea, and ¼ single.

29. A rose crossed with a pea produces 6 walnut and 5 rose offspring.

30. A walnut crossed with a single produces 1 single-combed offspring.

31. A walnut crossed with a walnut produces 1 rose, 2 walnut, and 1 single offspring.

32. If one of the walnut parents in the preceding question were crossed with one of its single-combed offspring, what would their offspring be like?

33. A rose crossed with a walnut produces offspring ⅜ of which are walnut, ⅜ rose, ⅛ pea, and ⅛ single. What are the genotypes of the parents?

34. A feather-shanked rose-combed crossed with a clean-shanked pea-combed one produces 25 feather, pea, offspring; 24 feather, walnut; 26 feather, rose; and 22 feather, single. What are the genotypes of the parents?

35. The offspring of a feather-legged pea-combed cock bred to a clean-legged pea-combed hen are all feather-legged. Most of them are pea-combed, but some singles appear among them. What are the genotypes of the parents? What would be the offspring expected from a cross of this hen with one of her feather-legged single-combed sons?

36. A right-handed blue-eyed man whose father was left-handed marries a left-handed brown-eyed woman from a family in which all the members have been brown-eyed for several generations. What offspring may be expected from this marriage, as to the two traits mentioned?

37. A brown-eyed right-handed man marries a blue-eyed right-handed woman.

Their first child is blue-eyed and left-handed. If other children are born to this couple, what will probably be their appearance as to these two traits?

38. A right-handed blue-eyed man marries a right-handed brown-eyed woman. They have two children, one left-handed and brown-eyed and the other right-handed and blue-eyed. By a later marriage with another woman who is also right-handed and brown-eyed, this man has 9 children all of whom are right-handed and brown-eyed. What are the genotypes of this man and his two wives?

39. A brown-eyed normal-minded man marries a brown-eyed normal-minded woman. Their first child is blue-eyed and feeble-minded. What is the chance that the next child will also show these same characteristics? (Normal mind, dominant.)

40. A breeder has a homozygous race of feather-legged, black, rose-combed birds and another of clean-legged, white, pea-combed ones. He wants a race of black birds that have clean legs and walnut combs. What proportion of the F_2 raised from a cross between these two races will be what he desires in appearance?

41. What are the phenotypes of the parents and offspring of the following cross: *ff Rr Pp* × *Ff Rr pp*.

42. In rabbits there are several factors that determine coat color:

C colored	*c* no color, albino
A ticked, agouti	*a* solid color, nonagouti
B black	*b* brown
S solid color	*s* spotted

(*AB*, agouti; *Ab*, cinnamon; *aB*, black; *ab*, brown)

An albino rabbit mated with a black produces agouti and black, spotted young. What factors are present in the albino parent and not in the black?

43. An agouti animal crossed with another agouti produces offspring of which $9/16$ are agouti, $3/16$ black, $3/16$ cinnamon, and $1/16$ brown. What are the genotypes of the parents?

44. What are the offspring of the following crosses? What are the appearances of the parents?

(*a*) *Cc Aa bb* × *cc aa Bb*
(*b*) *cc Aa Bb* × *CC aa Bb*

45. Two agouti rabbits produce 3 agouti and 1 black offspring. What are their genotypes? (Use only the *A,a* and *B,b* factors.)

46. In what two ways could you develop a pure-breeding strain of polled, black-bodied white-faced cattle?

47. Note.—In cattle the polled condition (*P*) is dominant over the horned (*p*); and in Shorthorns the heterozygous condition of red coat (*R*) and white coat (*r*) is roan.

If a homozygous polled, white animal is bred to a horned, red one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 with the polled, white parent? With the horned, red parent?

48. If a group of 100 polled, roan Shorthorn cows by horned bulls were mated to a roan bull that was heterozygous for the polled condition, what sort of offspring would you expect and in what numbers?

49. If a red-flowered broad-leaved plant is crossed with a white-flowered narrow-leaved one, what will be the appearance of the F_1 and the F_2?

50. If in mice you secured a 9 agouti: 3 black: 4 albino ratio in an F_2, what were the genotypes of the parents and the F_1 using the letter *C* to represent the gene

necessary for the expression of any color and A to represent the gene for banding of the black hairs with yellow to give the agouti pattern. What type of inheritance is this?

51. In cultivated stocks (a flower) gene C in the absence of gene R, produces cream-colored flowers; gene C with gene R, red ones; and genes cc with RR, Rr, or rr white flowers. If you crossed a red-flowered plant with a white and got an F_1 that was all red, what proportion of red, creams, and white flowers would you get in the F_2?

52. If you cross two spherical-shaped squash and secure a disk-shaped F_1 and then cross one of these F_1's to an elongated-fruit plant, what will be the fruit shape of their offspring?

NOTE.—In summer squashes the factor for white fruit color, W, is epistatic to that for yellow, Y; WY and Wy plants are white; wY plants yellow, and wy plants green.

53. What is the color of the fruit in the offspring of the following crosses, the genotypes of the parents being given?

$$Ww\,Yy \times Ww\,yy \qquad ww\,YY \times Ww\,yy \qquad Ww\,yy \times ww\,Yy$$

NOTE.—In the following three questions, which deal with fruit color in squashes, find the genotypes of the parents.

54. A white plant crossed with a yellow one produces offspring of which ½ are white, ⅜ yellow, and ⅛ green.

55. A white plant crossed with a green one produces offspring of which ½ are white and ½ yellow.

56. A white plant crossed with another white one produces offspring of which ¾ are white, $^3/_{16}$ yellow, and $^1/_{16}$ green.

57. What will be the flower color of the offspring of the following crosses, in which the genotypes of the parents are given?

$$Cc\,Pp \times cc\,Pp \qquad cc\,Pp \times CC\,pp$$
$$Cc\,Pp \times Cc\,PP \qquad Cc\,pp \times cc\,Pp$$

58. A white-flowered plant crossed with a purple produces offspring of which ⅜ are purple and ⅝ white.

59. A purple-flowered plant crossed with a white one produces offspring of which ½ are purple and ½ white.

60. A white-flowered plant crossed with another white produces offspring of which ¾ are white and ¼ purple.

61. In wheat, determine the genotypes of the parents in the following crosses:

(*a*) Red × white giving ¾ red and ¼ white.

(*b*) Red × red giving ⅞ red and ⅛ white.

62. How would you proceed in developing a feathered-shanked strain of poultry from clean-shanked birds?

63. If an F_2 yields a 15:1 ratio, what could you conclude as to the type of inheritance involved?

64. Write the genetic color formulas for two breeds of poultry both of which are white and the F_2 resulting from their crossing gives a 13 white:3 colored ratio.

65. Starting with two white breeds of poultry, how would you proceed to develop a true-breeding colored strain?

CHAPTER XIII

THE PRINCIPLES OF HEREDITY (*Continued*)

In the preceding chapter we have dealt with some of the more simple and clean-cut types of inheritance. During the past 30 years the inheritance of a great many traits in plants and animals has been studied and the methods of transmission from parent to offspring ascertained. The following might be called different types of inheritance, although basically there is but one type of inheritance, *viz.*, by means of genes. This method of inheritance is typical of all sexually reproducing forms, so that what may appear as different types of inheritance are actually different sorts of expressions of gene reactions. The procedure has been to cross plants or animals possessing different characteristics, tabulate the results by separate generations, and, finally, to construct a theory that would fit the observed facts. It should be noted that the facts come first and the theory to explain the facts comes later. This is the scientific approach. In animal breeding, we sometimes find people making the directly opposite approach, *i.e.*, starting out with a theory and trying to find facts that fit their theory. They generally do find some such facts, but unless one takes all the known facts into account, his contribution is apt to be nil. If one "selects" his facts carefully enough he can "prove" almost anything. Several typical forms of inheritance will be presented in the following sections.

Multiple Alleles.—Thus far we have spoken of only two alternatives as far as one pair of genes is concerned. We have talked about gene A or its allele, gene a. We have said, too, that the genes are probably complex, organic molecules made up of hundreds of thousands of atoms arranged spatially in some definite pattern. We assume too that the content and spatial arrangement of the atoms in gene A are different from those in gene a. It would seem logical, therefore, to expect that there might be more than two alternative arrangements. Breeding experience seems to indicate that there are.

If a colored rabbit, CC, is bred to an albino, c^ac^a, all the F_1 are colored, and in the F_2 there are 3 colored:1 albino. Likewise another cross, between colored, CC, and Himalayan, c^hc^h (white with black nose, ears, tail, and feet), gives an F_1 all of which are colored and the familiar 3 colored:1 Himalayan in the F_2. Now, if the cross is made between

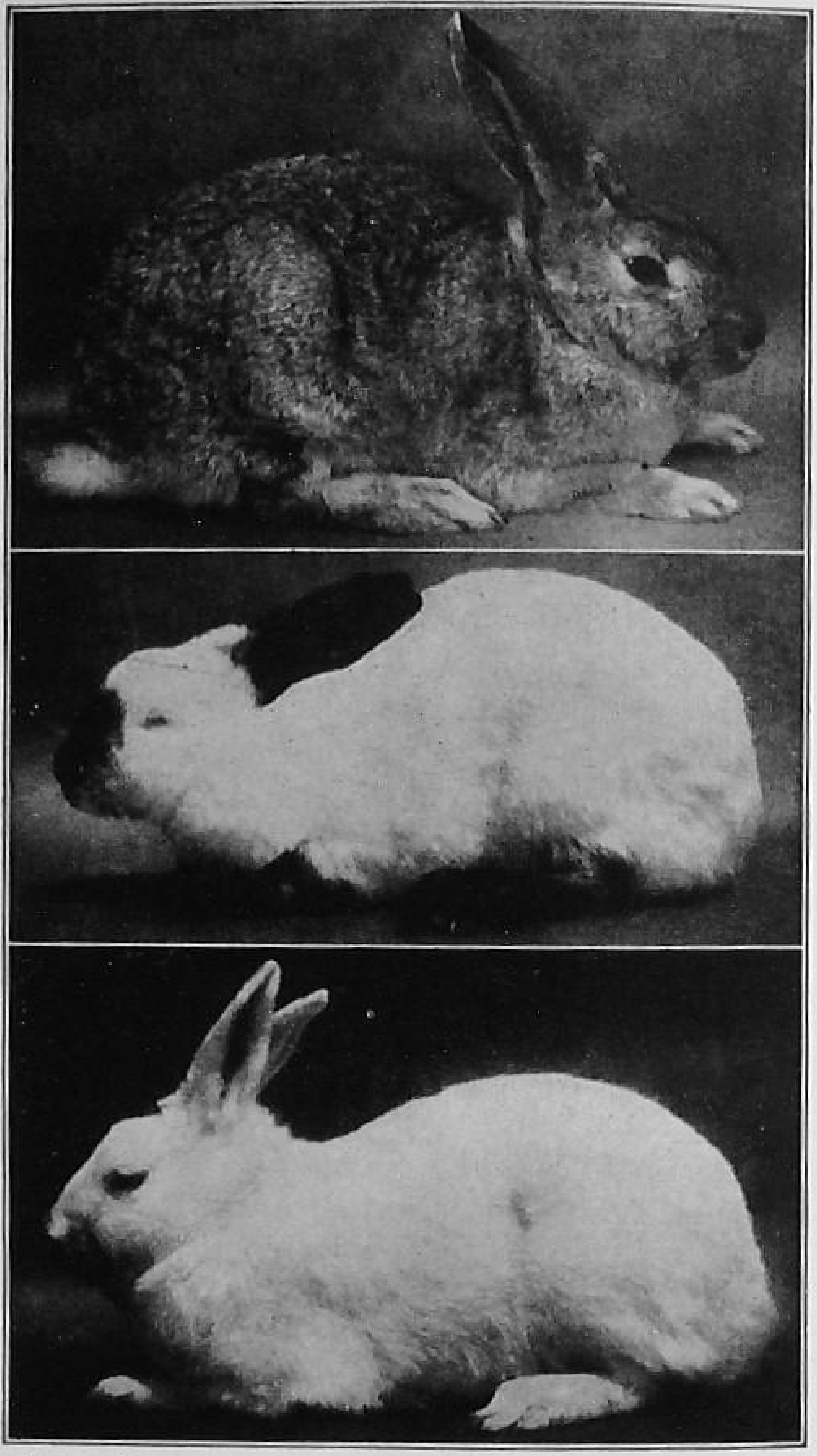

FIG. 97.—Three alleles of a gene for coat color in rabbits. Top, colored; center, Himalayan albinism; bottom, complete albinism. (*From Castle, in Journal of Heredity.*)

Himalayan, c^hc^h, and albino, c^ac^a, all the F_1 are Himalayan and in the F_2 there are 3 Himalayan:1 albino, which indicates but one pair of genes being involved. From the above breeding results, which show genes C and c^a to be allelic, genes C and c^h to be allelic, and genes c^h and c^a to be allelic, we conclude that all three genes C, c^h, and c^a form one multiple allelic series. Still another gene, c^{ch}, has been found in this series causing the chinchilla color or silvery gray with no yellow color in the fur, and this

has been found, as far as dominance is concerned, to fit in between genes C and c^h. Thus we could have the following genotypes.

colored rabbitt	CC, Cc^{ch}, Cc^h, Cc
chinchilla rabbit	$c^{ch}c^{ch}$, $c^{ch}c^h$, $c^{ch}c$
Himalayan rabbit	c^hc^h, c^hc
albino rabbit	cc

Many other multiple allelic series are known in both plants and animals, and in most of them dominance between the members below the wild-type dominant is lacking. In mice a multiple allelic series of four genes is known, gene C producing full color; gene c^{ch} dilute color or chinchilla; gene c^h extreme dilution; and gene c albinism, or lack of color. Here gene C is dominant over the other members of the series, but crosses between the other members give results intermediate between the two used, *e.g.*, crossing homozygous chinchilla with albino gives the intermediate, extreme dilution. Allelic series are known in many plants, and in Drosophila there are 14 alleles of the gene for red eye grading all the way down to white eyes. Series of multiple alleles are also known in guinea pigs, rats, mice, rabbits, and snapdragons.

In man, blood types show a multiple allelic series of three genes. Blood itself is not inherited, but type of blood is. The red-blood cells in man contain an antigen *A* or *B* or both. The blood serum contains antibodies *a* or *b* or both. A person of blood group *A* has antigen *A* in his red-blood cells and antibody *b* in his serum; of blood group *B* has antigen *B* in his red cells and antibody *a* in his serum; of blood group *AB* has antigens *A* and *B* in his red cells and neither antibody in his serum; and, finally, a person of blood group *O* has neither antigen *A* nor *B* in his red cells but both antibodies *a* and *b* in his blood serum. If, therefore, red cells from a person with the *A* antigen were introduced by blood transfusion into a person of type *B* with antibody *a* in his serum, the reaction between the serum antibody *a* and the red-cell antigen *A* would cause these cells to clump or agglutinate with possibly fatal results. In making blood transfusions, blood types must be ascertained in order to prevent red-cell agglutination.

TABLE 21.—BLOOD TYPES IN MAN

Type	Genetic make-up	Antigen in cells	Antibody in serum	Can give blood to	Can take blood from
A	*AA* or *Aa*	*A*	*b*	*A* or *AB*	*A* or *O*
B	A^BA^B or A^Ba	*B*	*a*	*B* or *AB*	*B* or *O*
AB	AA^B	*AB*	*o*	*AB*	All
O	*aa*	*o*	*ab*	All	*O*

Knowledge of the genetic make-up of individuals regarding blood type (Table 21) is sometimes useful in establishing possible, though not actual, paternity. If, for instance, a mother is of type *A* (genetic make-up *AA* or *Aa*) and her child is of type *O* (genetic make-up *aa* thus making mother *Aa*) and the assumed father turns out to be type *AB* (genetic make-up AA^B), this fact removes the possibility of his having actually been the child's father, because the child received two *a*'s and no man of type *AB* has an *a* to transmit to his offspring. If the tests revealed that the assumed father was of type *A*, *B*, or *O*, then the most that can be said is that he might have been the father as, of course, might also many other men.

Although many of the genes involved are not known to occur in multiple allelic series, the work of Irwin and his coworkers[1] demonstrating the presence of heritable antigens in the blood of cattle and several species of birds is of considerable interest. To date more than 40 such antigens have been detected in cattle blood. In addition to their interest from a basic genetic standpoint, they are useful in cases of disputed parentage in cattle.

Lethal Action of Genes.[2]—Any organism is a delicately balanced system of actions and reactions and can survive only a more or less limited range of change. This is nicely illustrated in the blood stream, which must maintain a proper balance of sugar, minerals, vitamins, hormones, and other elements if the organism is to function normally. All bodily characteristics are referable in the final analysis to the genes, which produced the organism, manifesting themselves of course in our internal and external environment.

It is not surprising, therefore, that gene changes sometimes result in the sort of unbalance that destroys the organism. Such manifestations are known as *lethals*. In the fowl, for instance, there sometimes occurs a condition known as *creeper* (short wings and legs). When two creepers are mated, some normal offspring are produced, the normal condition apparently being recessive to creeper, but the ratio of such matings is 2 creeper : 1 normal. Investigation has shown that some of the embryos die at about the fourth day of incubation, these presumably being homozygous creepers. Creeper, therefore, has the genetic constitution *Cc*, normal *cc*, this being a dominant lethal, according to Snyder, and the homozygous and heterozygous conditions are recognizably different.

Several recessive lethals are known in cattle, *viz.*, parrot-beaked (abnor-

[1] See Owen, R. D., *et al.*, An Immunogenetic Analysis of Racial Differences in Dairy Cattle, *Genetics*, **32**:64–74, 1947.

[2] See Eaton, O. N., A Summary of Lethal Characters in Animals and Man, *Jour. Hered.*, **28**(9):320–326, September, 1937.

mal lower jaw; calves live only a few hours), amputated (calves born dead with legs and lower jaw missing), short-spined (fused and compacted vertebrae), hairless. Bulldog calves with greatly dished faces and very short legs are a dominant lethal manifestation similar to creeper in fowl, the heterozygotes being the short-legged Dexter cattle.

Other abnormal conditions that may be due to lethal genes include mummified calves, resorbed fetuses, ossified joints, and various types of congenital dropsy. Other lethals in farm animals are known, *e.g.*, paralyzed hind limbs in sheep and swine, thick forelimbs, closed anus and cleft palate in swine, closed colon in horses. If an abnormal embryo is born the lethal is made obvious. Such happenings are generally due to failure to reach full development; *e.g.*, hair or limbs do not grow; palate, skull, or lips do not fuse in the mid-line; joints fail of full development with fluid and pads between bones. Lethals that destroy the organism in early embryonic life with its subsequent resorption may pass unrecognized as sterility.

Like most other mutations, the bulk of lethals are recessive and may remain hidden in a stock for many generations. For their total removal from a strain, test matings and rigid selection must be practiced with the knowledge that in the case of recessives both parents are carrying the gene.

Many lethals of various sorts are known also in plants and in man. Lethals may kill the organism at any time, *i.e.*, during embryonic, fetal, or postnatal times; and, if the lethal gene is located on the sex chromosome, peculiar sex ratios will of course result.

The following list of lethals contains those listed by Eaton[1] in 1937 and a few others reported in the *Journal of Heredity* since that time.

Horses

Atresia coli—closure of intestine	R*
Abnormal sex ratio—55 males: 90 females	Sex-linked R
Lethal white—low fertility—lethal or sterility factors or both	?
Stiff forelegs	Probably R

Cattle

Achondroplasia$_1$—(Bulldog) short legs and head, hernia, die and aborted fourth month	D†
Achondroplasia$_2$—(Bulldog) short head, cleft palate, deformed jaws, die soon	R
Acroteriasis congenita—amputated—appendages short or absent	R
Agnathia—very short lower jaw (sex limited to male?)	R
Ankylosis—ossification of joints	R

* R = recessive.
† D = dominant.

[1] *Loc. cit.*

Congenital dropsy—water in tissues and cavities . . . . R
Congenital ichthyosis—scaly, cracked skin . . . . R
Epitheliogenesis imperfecta—imperfect skin, partly hairless—septicemia . . . . R
Fetal resorption . . . . ?
Hernia cerebri—failure of frontal bones to fuse . . . . ?
Impacted molars—short jaw, defective teeth—die within week . . . . ?
Lameness in hind limbs—calves unable to stand . . . . R
Muscle contracture—head and legs drawn up—joints stiff . . . . R
Mummification—short, stiff neck, prominent joints—usually die as 8-months fetus . . . . R
Short limbs—limb short, hoofs undeveloped . . . . R
Short spine—ribs and vertebrae fused, back bent down . . . . R

Sheep

Amputated—no claws on feet . . . . ?
Earless and cleft palate . . . . R
Lethal gray—in Turkanas and Karakuls . . . . R
Muscle contracture—usually stillborn . . . . R
Paralysis—hind parts paralyzed—live few days . . . . R
Skeletal defects—large head, short upper jaw, rigid fetlocks . . . . R

Swine

Atresia ani—closed colon . . . . ?
Catlin mark—parietal or frontal bones not fused . . . . R
Cleft palate—young unable to nurse . . . . R
Excessive fatness—young die at 40 to 80 kg . . . . R
Fetal mortality . . . . R
Hydrocephalus—water outside brain in subarachnoid spaces . . . . . . R
Hypotrichosis—hairless (lack of iodine) . . . . ?
Legless—(shoulder blades and pelvic bones but no limb buds or leg bones) . . . . R
Lobed ear—usually also cleft palate and deformed hind legs . . . . Probably R
Muscle contracture—thick, stiff legs . . . . R
Paralysis—hind parts paralyzed . . . . R

Man

Brachyphalangy—short middle phalanx second finger and toe, live 1 year . . . . D
Congenital ichthyosis—cracked, imperfect skin, live 3 days . . . . R
Glioma retinae—malignant tumor of retina . . . . ?
Icterus—jaundice, live 4 days to 3½ years . . . . ?
Infantile amaurotic idiocy—degeneration of cerebrospinal nerves, live 2 or 3 years . . . . R
Progressive spinal muscular atrophy—live a few years . . . . ?
Xeroderma pigmentosum—sensitive skin, scars, and carcinoma, live 12 years . . . . R

Multiple Factors.—Thus far our discussion has been confined to qualitatively differing characters such as color of hair, presence or absence of

horns or of feathers, types of blood, or the ability or inability to survive, etc. There are many other characters, in fact most of the important ones, that do not exhibit this alternative type of expression but rather show all manner of gradation between rather wide limits. Such characters are quantitative and, as examples, size, yield, power, stamina, rapidity of fattening, quality of carcass, degrees of fertility, and probably most of the other commercially important characters of our livestock might be mentioned.

It seems probable that the final expression of a great many characteristics of higher animals may be due to the interaction of many sets of genes. This point of view has dawned gradually, as more detailed information about inheritance in some of the lower forms of life has accumulated, and is in direct contrast to the views held soon after the rediscovery of Mendel's work. Attempts have been made to analyze complex physiological processes such as milk production and the percentage of fat in milk on the basis of the interaction of a few pairs of genes, but they have not been successful. Fortunately, it should be possible to make progress in breeding on the basis of a sound knowledge of the basic principles even in the absence of specific information concerning the number and interactions of the genes responsible for the appearance of commercially valuable qualities. When many factors or genes are concerned, we know that the offspring arising from the mating of two extremes tend to fall on the average about midway between two parental levels. This principle is involved in indexing dairy bulls, as described in detail in Chap. XXI.

The multiple-factor hypothesis grew out of the work of Nilsson-Ehle with wheat and East with corn. The former crossed several strains of red and white wheats. In general the red color was only partially dominant over white, for the F_1 was not as dark red as the red parent. In the F_2 there were 3 reds (1 dark red, 2 lighter red) to 1 white. This indicates a one-gene pair reaction. Another cross of red and white wheats gave a similar F_1 but an F_2 of 15 reds (of varying shades) to 1 white thus indicating a two-gene pair reaction. Still a third cross gave the usual F_1 but an F_2 of 63 reds (again of varying shades) to 1 white, which indicates a three-gene pair reaction. This uniformity of the F_1 and variability of the F_2 is generally true of quantitative characters controlled by many genes. Breeding tests revealed that there were one, two, and three pairs of genes operating in these cases. In the two-gene cross it was shown that a wheat with four red genes was redder than one with three, this latter one redder than one with two, and this in turn redder than a wheat with only one red gene. In these cases, there is not complete dominance, but the genes act in a cumulative fashion.

This method of inheritance is now thought to be operative (along with

dominance, epistasis, and other types) in the inheritance of most of the commercially important animal characters. In other words, instead of color of wheat, we might substitute size, weight, yield, or many other quantitative traits. This will explain the difficulties encountered in attempting to unravel the exact mode of inheritance of many characters in the larger animals.

It is possible to determine with a fair degree of accuracy how many genes are operating to produce a given characteristic. If two extremes are mated, the F_1 will fall about midway between the parents if the genes are acting cumulatively. If 1 out of the 4 of the F_2 is as extreme as each of the 2 extreme grandparents, then we are justified in assuming that 1 pair of genes is involved. If 1 out of 16 of the F_2 is as extreme as each grandparent, then 2 genes must be operative. This interpretation fits very well the observed reactions of color inheritance in man, black skin being represented by *AA BB* and white skin by *aa bb*. The F_1 will be mulattoes, *Aa Bb*, and will yield five grades of color depending on the number of dominant genes present, *AA BB* being black, *AA Bb*, etc. being dark brown, *Aa Bb*, etc. being mulatto, *Aa bb*, etc., being light brown, and *aa bb* white.

A cross between long-eared rabbits (220 mm.) and short-eared (100 mm.) gives offspring with ears about 160 mm. in length. These F_1 rabbits in turn produce a graded scale of ear lengths in F_2 ranging from 220 down to 100 mm., each dominant gene accounting for an increased ear length of 20 mm. and acting cumulatively. The student should make up a table showing the number of operating genes on the basis of the number of extreme individuals in the F_2 and will find such a table useful in interpreting problems involving cumulative multiple-factor inheritance; 1 out of 4 as extreme as each grandparent = 1 pair of genes; 1 out of 16 = 2 pairs, 1 out of 64 = 3 pairs, etc.

On the basis of multiple-factor inheritance it is possible to make crosses that will yield some F_2 members more extreme than either grandparent. This is probably due to each parent contributing some effective alleles not supplied by the other parent and is known as *transgressive variation.* Thus one parent might be *AA BB cc* and the other *aa BB CC*, whereupon the F_1 would be *Aa BB Cc*, but giving the possibility of getting *AA BB CC* in the F_2, which would be more extreme than either grandparent.

Most quantitative characters such as size, growth rates, milk production, egg production, and prolificacy depend for their expression upon the interaction among a large but unknown number of heritable factors and environmental influences. Thus the evaluation of differences between breeds, lines, or strains of animals does not depend upon determining the actual effects of specific genes, but rather upon determining the average

effects of large numbers of genes. Because of the complexity of these interactions, standard statistical techniques are ordinarily necessary for the correct interpretation of genetic studies. A knowledge of such procedures as correlation, regression, and analysis of variance and covariance is necessary. The detailed statistical techniques are given in such standard texts as Snedecor (1946).

A question as to the scientific validity of the additive, nondominant action of multiple genes has recently been raised by MacArthur.[1] Using diallel crossing between four varieties of tomatoes with fruit weights ranging from 0.8 g. through 3.6, 65.9, and 106.8 g. per variety, this investigator found that the various F_1 hybrids were not an arithmetic average between the pure parent stocks but closely approached the geometric means of the parental varieties. For example, the cross between the 0.8-g. parent and the 3.6-g. parent did not yield an F_1 of 2.2 g. (the arithmetic mean) but the F_1 averaged 1.7 g. ($\sqrt{0.8 \times 3.6}$). Likewise the cross between the 3.6-g. and the 106.8-g. parents gave an F_1 of 19.4 g. (very close to $\sqrt{3.6 \times 106.8} = 19.6$) rather than the arithmetic mean of 55.2 g. The whole series of crosses was orderly and followed the geometric rather than the arithmetic pattern. The size of the F_1 fruits was quite evidently controlled to a large extent by the genes provided by the smaller parent or, stated differently, the amount of additional growth brought about by the genes of the larger parent was limited in a proportional manner by the substrate upon which the activating substances reacted. More recent work by MacArthur (1944 and 1949)[2] with mice appears to bear out his earlier conclusions based on tomato work.

Because so many of the commercially important characters of our livestock are dependent on cell size, cell number, or cell activity and appear to be controlled by many genes, this new theory, if it proves to be of general validity, will have an important bearing on our reasoning and procedures in livestock breeding. If, for example, 4,000-lb. producing cows were mated to a bull with a hereditary complex for 24,000 lb. of milk, we would expect the resulting daughters to average not halfway between 4,000 and 24,000 or 14,000 lb. (the arithmetic mean) but rather at 9,800 lb. ($\sqrt{4,000 \times 24,000}$). In other words, the genes from this very high-heredity sire are limited proportionally by the low-heredity genes of the dams. Where the differences in the hereditary levels are

[1] MacArthur, J. W., Size Inheritance in Tomato Fruits, *Jour. Hered.*, **32**(9): 291–295.

[2] MacArthur, J. M., Genetics of Body Size and Related Characters. I. Selecting Small and Large Races of the Laboratory Mouse, *Amer. Nat.*, **78**:142–157, 1944; II. Satellite Characters Associated with Body Size in Mice, *Amer. Nat.*, **78**:224–237, 1944; Selection for Small and Large Body Size in the House Mouse, *Genetics*, **34**:194–209, 1949.

small, the arithmetic and geometric means are very similar. For example, if the sire's level was 14,000 lb. and the dams 12,000 lb., the arithmetic mean would be 13,000 and the geometric mean 12,961 lb.

Sex-linked Inheritance.—In the examples used thus far to illustrate various types of inheritance, it has made no difference as to sex where the various characteristics were placed; *i.e.*, this set could have been in the male, that in the female, or vice versa. In the type now to be discussed, however, it will make a difference, because the genes determining the characteristics will be located in the chromosomes that determine the sex of the individual.

Drosophila melanogaster, the common fruit fly, has provided more material assistance than any other species in the solution of the problems involved in hereditary transmission. Cytological studies of the cells of this organism reveal the fact that they have four pairs of chromosomes. In the female, these are all evenly paired, two of the pairs being large, bent rods; one pair very small and oval-shaped; and one pair fairly large, straight, and rod-shaped. The first three pairs are called *autosomes*, and the last pair sex or X chromosomes (see Fig. 89). The chromosomal make-up of males is similar to that of females regarding the autosomes but the male has an odd pair, one of the pair being an X chromosome, like that found in duplicate in the female, the other member of the pair being somewhat smaller, with a hook or bent portion at one end, and called the Y chromosome.

XY Type of Sex Inheritance.—In the breeding work with Drosophila, which normally have red eyes, a white-eyed mutant male was found by Morgan. This male was saved and, when mated to red-eyed females, yielded an F_1 all of which were red-eyed. The F_2 gave the expected 3 red:1 white phenotypic ratio, but it was noted that the white-eyed individuals were all males. This exception to usual Mendelian expectancy was finally explained by locating the gene for white eyes in the X chromosome. The F_1 female from a red-female white-male cross would therefore have two chromosomes, in one of which would be found the gene for red eyes, with the gene for white eyes in the other sex chromosome. Mated to a red-eyed male, she in turn would yield an F_2 with both of the females red-eyed, one male red-eyed, and the other white-eyed. The diagram on page 349 illustrates this cross.

This is an example of sex-linked inheritance. It is seen that the female produces eggs, following reduction, all of which are alike as far as the sex chromosome is concerned, whereas the male produces two sorts of sperm cells in equal numbers, one containing an X chromosome and the other a Y chromosome. The sex of the offspring depends, therefore, on the type of spermatozoon that happens to fertilize the egg, an X egg plus an

X-containing sperm yielding a female and an X egg plus a Y-containing sperm yielding a male. All characteristics that are determined by genes carried in the X chromosomes will, therefore, show this peculiar type of sex-linked inheritance. Many such characteristics have been discovered and catalogued.

White-eyed male sperms	Red-eyed female eggs		
	*R*X	*R*X	
*r*X	*R*X*r*X	*R*X*r*X	F_1 red-eyed females, heterozygous
Y	*R*XY	*R*XY	F_1 red-eyed males

and the F_2 produced by mating two F_1's

Red-eyed male sperms	Red-eyed female (heterozygous) eggs		
	*R*X	*r*X	
*R*X	*R*X *R*X	*R*X *r*X	F_2 red-eyed females, 1 heterozygous
Y	*R*XY	*r*XY	F_2 males, 1 red-eyed, 1 white-eyed

FIG. 98.—Checkerboard diagram of cross of red-eyed female and white-eyed male through F_2.

Sex-linked Factors in Drosophila.—There is abundant substantiating proof of this theory from the behavior of sex-linked factors. The sex chromosomes (chromosome I in the chart, Fig. 108) carry factors that determine characteristics just as do the other chromosomes. About 200 sex-linked characters have been discovered in the fruit fly. The factor for white eyes in Drosophila, for instance, is sex-linked. When a white-eyed male *r*XY is mated to a red-eyed female *R*X*R*X, the F_1 offspring all have red eyes, because red eye is dominant to white eye in Drosophila. In the F_2, red- and white-eyed flies are produced in the proportion of 3 red:1 white. All the females of this generation are red-eyed, but of the males ½ have red eyes and ½ have white eyes. When the reciprocal cross is made, *i.e.*, when a white-eyed female is mated to a red-eyed male, the results are different. In the F_1 of such a mating, all the female flies have red eyes and all the male flies have white eyes. In the F_2 of this cross, ½ the females have red eyes and ½ have white eyes, and likewise among the males ½ have red eyes and ½ have white eyes.

	rX	Y
RX	$RXrX$	RXY
RX	$RXrX$	RXY

F_1 cross, white-eyed male and red-eyed female

↓

	RX	Y
RX	$RXRX$	RXY
rX	$RXrX$	rXY

F_2 cross, white-eyed male and red-eyed female

	RX	Y
rX	$RXrX$	rXY
rX	$RXrX$	rXY

F_1 cross, red-eyed male and white-eyed female

↓

	rX	Y
RX	$RXrX$	RXY
rX	$rXrX$	rXY

F_2 cross, red-eyed male and white-eyed female

Fig. 99.—Diagram of cross of white-eyed male × red-eyed female and the reciprocal.

In the foregoing diagrams the presence of two X chromosomes determines a female, an X and a Y chromosome determine a male. The presence of at least one R determines red eyes, because red eye is dominant to white. It has been pointed out previously that, aside from the pair of sex chromosomes, the pairs of chromosomes in both the male and the female of Drosophila are alike and carry corresponding factors or determiners of characteristics. In this type of sex inheritance, the female is homogametic for the sex chromosome. A variation of the XY type of sex determination occurs in some species that lack the Y chromosome. Here the females are XX but the males are XO (Y chromosome lacking). It is evident, however, that the male will still produce two types of spermatozoa, one containing an X chromosome, the other lacking an X chromosome.

Sex-linked Characters in Man.—In the human family a sex-linked characteristic is that of color blindness, or the inability, through an inherent defect in the eye, to distinguish between various colors. It is well known that there are many more color-blind men than women, the reason for which should soon be evident. Representing normal vision with C and color blindness with c, the following is the genetic make-up of a normal-visioned woman $CXCX$ and of a color-blind man cXY. Such mating would give children in the F_1 all of whom would be normal-visioned, though all the daughters would be carriers of color blindness. In the F_2, there would be 3 normal-visioned children (2 daughters and 1 son) to 1 color-blind child (son). The reciprocal cross is also diagramed as shown in Fig. 100.

In the foregoing, two X chromosomes determine a female, an X and a Y chromosome determine a male, and at least one C determines the ability to differentiate colors. The occurrence of color-blind men is to

be expected more frequently than color-blind women, for a double dose of the color-blind gene is necessary to produce a color-blind woman (*e.g.*, if 10 per cent of males were color-blind, then we could expect 0.1×0.1 or approximately 1 per cent of women to be color-blind).

Recent work has shown that, at least in man and possibly in one or two rodents, portions of the Y chromosomes are homologous with portions of the X chromosomes. These regions carry allelic genes and synapse during the maturation processes. Chiasmata form and crossing over takes place between them. Genes located in these regions are called "partially sex-linked."

	cX	Y
CX	CXcX	CXY
CX	CXcX	CXY

F_1 cross, color-blind man and normal-visioned-woman

	CX	Y
cX	CXcX	cXY
cX	CXcX	cXY

F_1 cross, normal-visioned man and color-blind woman

	CX	Y
CX	CXCX	CXY
cX	CXcX	cXY

F_2 cross, color-blind man and normal-visioned woman

	cX	Y
CX	CXcX	CXY
cX	cXcX	cXY

F_2 cross, normal-visioned man and color-blind woman

FIG. 100.—Diagram of cross of color-blind man and normal-visioned woman and its reciprocal.

WZ Type of Sex Inheritance.—Another type of sex inheritance, which, to distinguish it from the XY type, is called the WZ type, is found in poultry. Here the distinguishing feature is the fact that the male is homogametic for the sex chromosome, whereas the female is heterogametic. According to Castle, this condition is found in moths and in certain fish and birds; *e.g.*, in domestic fowls, pigeons, ducks, and canaries.

A well-known example of sex-linked inheritance in poultry is that of coat pattern. For instance, if a Plymouth Rock (barred) cock is mated to a black (or any other nonbarred breed), the F_1 offspring, both male and female, are barred. When these F_1 hybrids are mated, producing the F_2 generation, there results 3 barred individuals (2 males and 1 female) to 1 nonbarred or black (female). When the reciprocal cross is made, *viz.*, black cock mated to barred hens, there are produced in the F_1 barred males and nonbarred, or black, females. When these F_1 hybrids are mated, producing the F_2 generation, ½ the number of males so produced are barred and ½ are black, and of the females ½ are barred and ½ are black. Diagrammatically, we have *B*, barred; *b*, black; ZZ, male; ZW, female.

	BZ	*BZ*
bZ	*BZbZ*	*BZbZ*
W	*BZW*	*BZW*

F_1 cross, barred cock and black hen

	bZ	*bZ*
BZ	*BZbZ*	*BZbZ*
W	*bZW*	*bZW*

F_1 cross, black cock and barred hen

	BZ	*bZ*
BZ	*BZBZ*	*BZbZ*
W	*BZW*	*bZW*

F_2 cross, barred cock and black hen

	BZ	*bZ*
bZ	*BZbZ*	*bZbZ*
W	*BZW*	*bZW*

F_2 cross, black cock and barred hen

FIG. 101.—Diagram of cross of barred cock and black hen and its reciprocal in F_2.

In the foregoing, two *Z*'s determine a male, one Z and one W a female, and at least one *B* a barred individual.

In some species the Y or W chromosome is lacking, giving XO or ZO types of spermatozoa or ova.

Sex-influenced Inheritance.—This type of inheritance is not to be confused with sex-linked inheritance, which has been discussed in the previous sections. In sex-linked inheritance the genes determining the characteristic are located in the X chromosome. Such is *not* the case in sex-influenced characters, the genes for such characteristics being located in the autosomes, *not* in the sex chromosomes.

Basically all characteristics are dependent on genes, or the interaction of genes plus, of course, a suitable environment, both external and internal. The environment, be it noted, is just as important as the genes. A cow, for instance, might have inherited the genes that would allow her to produce 10,000 lb. of milk under good environmental conditions, but, if she calves out in the woods and runs wild therein, it is doubtful whether she would give more than a few hundred pounds of milk at the most.

Animals also have an internal environment, their own bodies, and it is apparently this internal environment that, together with genes, is the determining factor in the expression of sex-influenced characteristics. Both the male and the female are supplied with several sets of glands that secrete chemical substances which are picked up by the blood stream and carried to all parts of the body, where they make their presence known through influencing the activities of cells in various parts of the body. These are known as the *endocrine*, or *ductless*, glands, and their secretions as *hormones*. The thyroid gland, which lies athwart the Adam's apple, secretes thyroxin, which plays a very important part in

both physical and mental growth. The suprarenal capsules, situated just above the kidneys, secrete adrenalin, which helps to regulate the amount of sugar in the blood. The most important of these ductless glands is probably the pituitary gland, which lies embedded in a little bony socket at the base of the brain and is known to secrete a dozen or more hormones, among others those which incite and regulate sexual manifestations as well as lactation. The gross picture, as far as the above endocrines are concerned, is the same for both male and female.

However, the female has ovaries and the male testes, and, as was noted earlier, these glands have an endocrine as well as a spermatogenetic or ovogenetic function. In other words, the internal environment of males and females is basically different, and herein lies the explanation of the expression of these so-called "sex-influenced" characteristics. In sheep, for instance, some breeds have horns in both sexes, some horns in the males only, and still other breeds are hornless in both sexes. If we crossed a horned breed (*hh*) with a hornless one (*HH*), the F_1 males will be horned (*Hh*) and the F_1 females (*Hh*) hornless. If we go on and get the F_2 from this cross, we find that among the males there is a ratio of 3 horned:1 hornless, among the females a ratio of 3 hornless:1 horned. Clearly the internal environment is influencing the expression of this characteristic. Warwick and Dunkle[1] have shown that genes *H* (hornlessness), *H'* (Dorset horns, *i.e.*, in both sexes) and *h* (Merino and Rambouillet horns, *i.e.*, horns in male, knobs in female) form a series of multiple alleles.

A somewhat similar situation is found regarding the inheritance of the very dark red (mahogany) color in Ayrshire cattle, the *Mm* genotype producing mahogany and white pattern in males, but red and white in females. In man, a certain type of baldness shows the same sort of inheritance.

Male		Female
mahogany and white	*MM*	mahogany and white
mahogany and white	*Mm*	red and white
red and white	*mm*	red and white

Still another sort of sex-influenced inheritance is that relating to cock and hen feathering in poultry. As is well-known, the differences in the plumage patterns between males and females are due to testicular and ovarian hormones. If the ovary of a bird belonging to a race that normally exhibits differences in male and female plumage is removed and a piece of testes transplanted into her, she will then proceed to develop

[1] See *Jour. Hered.*, **30**(8):325–329.

the male feather pattern. A dominant gene (H) for hen feathering is known in poultry. Hens of whatever genetic constitution (HH), (Hh), or (hh) will be hen-feathered because they lack the proper internal environment, specifically the male sex hormone, to produce cock feathering. In males, the gene H prevents the development of cock feathering so that HH and Hh males are hen-feathered, whereas hh males are cock-feathered. The characteristic is therefore seen to be sex-limited to the male and to be due to the interactions of genes with the internal environment of the animal.

Probability.—Mathematics is coming to play a greater and greater part in genetic research owing to the fact that inheritance is traceable to particulate elements, genes, which, although functioning through a complex system of reproductive physiology, yet behave in an orderly, specific, predictable manner. Mendel's early success in discovering the basic laws of inheritance was due largely to the fact that he kept accurate records of the appearance of characteristics by separate generations and found that they followed a certain statistical regularity.

If we toss a penny, it has an even chance of falling heads or tails, the chance of its falling either being $\frac{1}{2}$. If we toss two pennies, the chance that one of them will fall heads is $\frac{1}{2}$, the chance that the other will fall heads is $\frac{1}{2}$, and the chance that both will fall heads is the product of the likelihood of each separate event or $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. The same situation prevails for the likelihood of both falling tails. The chance that one will fall heads and the other tails is $\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$, or that the former will fall tails and the latter heads is $\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$, so that the chance of getting one head and one tail simultaneously is $\frac{1}{4} + \frac{1}{4}$ or $\frac{1}{2}$. Likewise if we toss three pennies we may get all heads, in fact, the chance that we will is definitely known to be $\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$ or 1 chance in 8, and the chance that we will get two heads and one tail is again the product of the separate probabilities; *i.e.*, two heads $= \frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4} \times$ one tail $= \frac{1}{2}$ or $\frac{1}{8} \times 3 = \frac{3}{8}$, because with three coins being tossed the two-heads-and-one-tail combination can appear from any of three combinations. Likewise, we would have a $\frac{3}{8}$ chance of getting one head and two tails and a $\frac{1}{8}$ chance of getting three tails.

This is seen to be simply an expansion of the bionomial $(a + b)^n$, where $a = \frac{1}{2}$ and $b = \frac{1}{2}$ and n is any number. We can let a represent heads (chance $\frac{1}{2}$) and b represent tails (chance $\frac{1}{2}$). Therefore, we can quickly find the answer to the question, "How many times in tosses of three coins simultaneously will we get two heads and one tail? Expanding the bionomial we have $a^3 + 3a^2b + 3ab^2 - b^3$. Since we are dealing with the two heads and one tail combination and a stands for heads and b for tails, we select the second term of the expansion $3a^2b$ and substitute

the values for a, ($\frac{1}{2}$) and for b, ($\frac{1}{2}$) and we have $3 \times (\frac{1}{2})^2 \times \frac{1}{2}$ or $3 \times \frac{1}{4} \times \frac{1}{2} = \frac{3}{8}$.

The procedure is the same for any problem involving probabilities; *viz.*, first find the probability of each separate event and then substitute these values in the proper term of the expanded bionomial. If, for instance, we wanted to know how many times in clutches of 8 eggs from birds that are heterozygous for both A and B, *i.e.*, of the genetic constitution $Aa\ Bb$, we would get 6 feather-shanked and 2 clean-shanked birds, first, we must remember that these are duplicate factors and that either A or B or both will produce feathered shanks, while $aa\ bb$ is clean-shanked. The ratio from these parents is then 15 feathered:1 clean. We will let a stand for feathered and b for clean. Now our term in the bionomial expanded to the eighth power is $a^8 + 8a^7b + 28a^6b^2$, and we now substitute the values for a and b, giving $28\left(\frac{15}{16}\right)^6\left(\frac{1}{16}\right)^2 = \frac{318{,}937{,}500}{4{,}294{,}966{,}296}$, or roughly $\frac{1}{13}$. In other words, once out of 13 times we can expect to get 6 feathered and 2 clean-shanked birds from clutches of 8 eggs when the parents are double heterozygotes for the two pairs of genes that act in a duplicate fashion in producing this characteristic.

In cases where there are three possibilities, *e.g.*, in a cross between two red hogs that are double heterozygotes for the two pairs of genes either dominant of which by itself produces sandy-colored hogs in a 9:6:1 ratio, we would have to expand the trinomial $(a + b + c)^n$.

In all cases the chromosomes assort and recombine at random according to the laws of probability.

Gene Manifestations.—Genes are the genetic representatives of specific characteristics. The exact nature of the physicochemical make-up of the genes is unknown. At present, they are known simply by their actions. It is the purpose here to point out some of the ways in which factors manifest themselves.

The simplest gene manifestation is of the sort where apparently one gene conditions the development of a certain characteristic, *e.g.*, the factor P, which brings about polledness in cattle. As a contrast to this may be considered the function of milk production, which is no doubt dependent on a great many genes, for milk production is a complex physiological phenomenon dependent among other things on the capacity, temperament, and vitality of the cow. One gene may have a very pronounced effect on the individual; *e.g.*, in peas, the gene T, which brings about tallness, whereas genes tt bring about dwarfness; or the gene may cause the early death of the individual (lethal genes). On the other hand, the gene may condition the development of a minor characteristic, such as eye color. The white eye in Drosophila, however, is only one of the several

characters that such mutants exhibit, some of the others being a lowered fertility and vitality; thus, one gene apparently affects many characteristics. The individuals of certain races may exhibit a good deal of variability, but the evidence would seem to point not to the unstable nature of the gene but rather to environmental effects as the source of this variability.

Entirely different genes may also bring about the identical characteristic in the organism.[1]

> We find, in experience, that we cannot safely infer from the appearance of the character what gene is producing it. There are at least three white races of fowls, produced by different genes. We can synthesize white-eyed flies that are somatically indistinguishable from the ordinary white-eyed race, yet they are the combined product of several known color-producing genes. The purple eye color of Drosophila is practically indistinguishable from the eye colors maroon and garnet.

It should be emphasized that determiners are not characteristics. An animal does not inherit characteristics from its ancestors, but rather it does inherit potentialities. Whether the potentiality develops to its fullest extent in the animal depends upon the environment, and the term *environment* is here used in its widest sense. The new organism has an environment from the minute the egg is fertilized by the sperm; or we might go even further back and consider that the egg and sperm each has an environment before fertilization has been accomplished. The point is that the environment, speaking generally, may inhibit the full expression of potentialities from a time preceding fertilization until physiological maturity has been attained. Developmental aberrations in utero may affect the embryo deleteriously from either an anatomical or a physiological standpoint; and the same is true of a multitude of environmental conditions following birth. For example, even though an animal inherited the potentiality for large body size or high milk production, the end results actually obtained are capable of extensive modification through feeding and management. Likewise many people inherit the potentiality for having considerable pigment in their skin, but this is conditioned by the action of sunlight. In other words, we tan in summer and bleach in winter.

The Gene.—Up to the present, genes are known only indirectly; *i.e.*, we know them by their actions. That they are chemical structures of some sort is, of course, a generally accepted opinion. Mendel postulated some sort of entities within the germ cells that were held responsible for the appearance of certain somatic characters. Later genetic studies sub-

[1] MORGAN, T. H., "Physical Basis of Heredity," pp. 239–240, J. B. Lippincott Company, Philadelphia, 1919.

stantiated this idea, and the genes for many characters have been definitely located in certain chromosomes in relation to other genes in the same chromosome on the basis of their behavior in hereditary transmission. In brief, the gene is thought of as an organic unit, located in a definite place in the chromosome, which is in some manner capable of reproducing itself, and the genes in turn are held to be the responsible agents in making possible the appearance of all the characteristics of a new organism.

Various estimates have been made regarding the size of the gene, ranging from 10 to 70 mμ as the upper limit. In any event they must be exceedingly minute. Because of the fixed wave length of visible light, the smallest objects that can be seen distinctly with the highest powers of the microscope[1] are of the order of 250 mμ, *i.e.*, about 1/100,000 in. (1/100,000 in. compares with 1 in. as 1 in. compares with 1.58 mi.) By use of the ultraviolet light with its shorter wave length, objects of the order of 100 mμ have been photographed. Ordinary bacteria, without distinguishable nuclei or chromosomes but presumably containing genes, are of the order of 500 to 750 mμ, and the filterable viruses are thought to be of the order of about 10 to 250 mμ.

Summary.—In this chapter we have considered several additional types of inheritance. We have learned that there may be more than two alternative forms of a gene making manifest the principle of multiple alleles. We also have seen that many of the commercially valuable characters of our animals are determined by the interactions of a great many pairs of genes. It is this feature, plus the fact that our larger animals have so few offspring, that makes animal breeding so difficult. We have also become acquainted with the action of lethal genes as well as the various types of inheritance associated with or dependent upon the sex of the individuals. Finally, we have seen that the transmission of potentialities from ancestors to offspring behaves in an orderly fashion which is predictable on the basis of the laws of chance or probability, that the final result of gene action may follow a variety of patterns, and that cytology is working ever closer to a satisfactory explanation of the nature of the basis of all living matter, the gene.

References[2]

Problems

1. If two chinchilla rabbits produce both chinchilla and albino offspring, what are the genotypes of all these animals?

2. Could two chinchilla rabbits produce both Himalayan and albino offspring?

[1] The current development of the electron microscope may soon permit much more detailed physical knowledge of the chromosomes and genes.

[2] See lists at end of Chaps. XI and XII.

3. What are the genotypes of the parents in the following rabbit crosses:
(*a*) Colored × colored give 3 colored and 1 albino.
(*b*) Colored × chinchilla give ½ colored; ¼ chinchilla; ¼ Himalayan.
(*c*) Chinchilla × Himalayan give ½ chinchilla; ½ Himalayan.
(*d*) Colored × Himalayan give ½ colored; ½ Himalayan.
(*e*) Chinchilla × Himalayan give ½ chinchilla; ¼ Himalayan; ¼ albino.

4. What will be the phenotype, as to blood groups, of offspring of parents of the following genotypes for blood groups:

$$Aa \times a^b a$$
$$Aa^b \times a^b a$$
$$a^b a \times a^b a$$

5. If a person of blood group *AB* marries one belonging to group *O*, what will be the blood groups of their children?

6. Note.—In the three following problems on blood groups, determine the genotypes of the parents.

One parent is group *A* and the other group *B*, but all four groups are represented among the children.

7. Both parents are group *A*, but ¾ of the children belong to group *A* and ¼ to group *O*.

8. One parent is *AB* and the other *B*, but of the children ¼ are *A*, ¼ *AB*, and ½ *B*.

9. In the two following cases of disputed paternity, determine the true father of the child: (*a*) The mother belongs to group *B*, the child to *O*, one possible father to *A* and the other to *AB*. (*b*) the mother belongs to group *B*, the child to *AB*, one possible father to *A* and the other to *B*.

10. In the choice of donors for blood transfusion, a patient's brother or sister is often selected. Would these be more likely to be successful donors if both parents belonged to blood group *AB* or if both belonged to group *O*? Explain.

11. If both parents belong to blood group *AB*, what proportion of their children would be expected to be of such a type as to be able to give blood to their parents?

12. Consult the chromosome map for Drosophila (p. 357) and determine how many dominant genes must be present in each chromosome to give the normal red eye color.

13. If a rose-combed creeper male is mated to a rose-combed creeper female and produces a number of single-combed normal birds, what were the genotypes of the parents?

14. Note.—In poultry, creeper is a semidominant lethal, barring a sex-linked dominant.

A cross of creeper, barred female and normal, nonbarred male would give what offspring?

15. A cross of creeper, heterozygous barred male and creeper, nonbarred female would give what offspring?

16. A cross of creeper, double-heterozygous walnut-combed, barred female and normal, rose-combed, heterozygous barred male would give what offspring?

17.* A sex-linked recessive lethal factor is known in poultry. What would be the sex ratio of the offspring of a male, heterozygous for the lethal, crossed with normal females?

* Note.—In this list the problems that are starred are taken from Snyder, "Principles of Heredity," D. C. Heath and Company, Boston, 1940, and are reproduced here through the kind permission of the author and publishers.

18.* In a certain series of matings between normal pigs, 38 offspring were born. Of these 29 were normal, and 9 had greatly swollen forelegs. The latter lived only a few hours. How could these results be explained genetically?

19.* In the Tzouracana sheep of Romania, gray individuals and black individuals are found. The black animals when bred together give all black offspring. Black mated to gray results in approximately equal ratios of black and gray lambs. When grays are mated together, approximately two-thirds of the offspring are gray, and one-third black. What kind of inheritance appears to be involved?

20.* In a certain strain of Oldenburger horses, tracing back to the mare, Jelka, the females of the line regularly produce only half as many male offspring as female offspring. What genetic explanation can you suggest for this?

21.* In cattle, the polled condition is dependent upon a dominant factor (P), the horned condition upon its recessive allele (p). In the Dexter-Kerry cattle the short-legged (Dexter) condition is dependent upon a dominant lethal factor (D), the long-legged (Kerry) condition upon its recessive allele (d). Suppose a Dexter bull homozygous for polled were mated to a horned Dexter cow. What kinds of calves could they produce, and in what proportions?

22.* Suppose two polled Dexter animals were mated and produced a horned Kerry calf. What would be the genotypes of the parents?

23.* What kinds of offspring would be expected from the mating of two horned Kerry animals? Two horned Dexter animals?

24. Note.—Assume that in man the difference in skin color between Negro and white is due to two pairs of factors; that $AA\ BB$ is "black" and $aa\ bb$ "white"; and that any three of these factors produce "dark" skin; any two, "medium"; and any one "light."

What will be the skin color of the offspring from a mating of white with black? From a mating of two individuals genotypically like these F_1 offspring?

25. What are the genotypes of the parents in the two following matings of Negroes: medium × light, giving $\frac{1}{8}$ dark, $\frac{3}{8}$ medium, $\frac{3}{8}$ light, $\frac{1}{8}$ white; median × light, giving $\frac{1}{2}$ medium and $\frac{1}{2}$ light?

26.* A variety of squash bearing 6-lb. fruits is crossed with one bearing 3 lb. fruits. The F_1 plants bear $4\frac{1}{2}$ lb. fruits. Among the F_2 fruits there is considerable variation, but out of 200 such fruits there are three which weigh as little as 3 lb., and three which weigh 6 lb. How many pairs of factors are responsible for the difference in weight between the two parent lines, and how much does each effective allele contribute to this difference?

27.* How many different homozygous strains bearing 4-lb. fruits could be developed?

28.* A race of oats yielding 10 g. per plant was crossed with a race yielding 4 g. per plant. The F_1 plants yielded 7 g. per plant. Out of 253 F_2 plants, four yielded as much as 10 g. per plant and four yielded as little as 4 g. per plant. How is yield inherited in these oats?

29.* In the preceding problem, how much does each effective allele contribute to yield?

30.* Two different races of corn each averaging 68 in. in height were crossed. The F_1 also averaged 68 in. in height. In the F_2, however, there was considerable variation, ranging from 36 to 100 in. Out of 1,942 F_2 plants, eight reached a height of 100 in., and seven were as short as 36 in. Explain these results in terms of genetic factors, assuming that the environment was held similar for these plants.

Note.—Color blindness and hemophilia in man are sex-linked recessives.

31. A girl of normal vision whose father was color-blind marries a man of normal vision, whose father was also color-blind. What types of vision will be expected in their offspring?

32. A color-blind man marries a woman of normal vision. They have sons and daughters, all of normal vision and all of whom marry normal persons. Where among the grandchildren may color blindness be expected to appear? If there are cousin marriages among these grandchildren, where among their offspring may color blindness be expected to appear?

33. A man and woman, both of normal vision have (*a*) a color-blind son who has 1 daughter of normal vision: (*b*) a daughter of normal vision who has 1 color-blind and 1 normal son; and (*c*) another daughter of normal vision who has 5 sons, all normal. What are the probable genotypes of grandparents, children, and grandchildren?

34. A brown-eyed woman with normal vision whose father was color-blind and blue-eyed marries a man who is blue-eyed and of normal vision. What offspring may this couple expect as to eye color and vision?

35. A man (A) with hemophilia marries a normal woman (B). Their daughter (C) marries a man (D) with hemophilia and produces 2 sons, 1 (E) with hemophilia. The normal son (F) marries a woman (G) whose paternal grandfather (H) has hemophilia but whose parents (I and J) were apparently normal. What are the genotypes of all the individuals concerned?

36. A man's maternal grandmother had normal vision; his maternal grandfather was color-blind; his mother is color-blind; his father is of normal vision. What are the genotypes, as to vision, of the two parents and grandparents mentioned? What type of vision has this man himself? What type have his sisters? If he should marry a woman genotypically like one of his sisters, what type of vision would be expected in the offspring?

37. The mother of a right-handed brown-eyed woman of normal vision is right-handed, blue-eyed, and of normal vision, and her father is left-handed, brown-eyed, and color-blind. This woman marries a man who is left-handed, brown-eyed, and of normal vision whose father was blue-eyed. What chance will the sons of this couple have of resembling their father phenotypically?

38. What effect on the sex ratio would a recessive sex-linked lethal factor have in man?

NOTE:—Barred plumage in poultry is a sex-linked dominant.

39. In poultry, if a nonbarred cock is crossed with a barred hen, and an F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offpsring of these last two crosses, as to barring?

40. A single-combed barred cock crossed with a walnut-combed barred hen produces the following offspring:

4 rose, barred males.
5 walnut, barred males.
2 rose, barred females.
3 rose, nonbarred females.
2 walnut, barred females.
2 walnut, nonbarred females.

What are the genotypes of the parents?

41. In poultry, assume high egg laying to be determined by two factors, one of which, M, is sex-linked and the other, L, not sex-linked. A breeder has two high-

producing hens and five males of unknown genotypes. Each hen is bred to each male with results as follows:

Hen 1 × male 1 gives ⅜ high, ½ medium, and ⅛ low layers.
Hen 1 × male 2 gives ¼ high, ½ medium, and ¼ low.
Hen 1 × male 3 gives ½ high, ½ medium.
Hen 1 × male 4 gives ¾ medium, ¼ low.
Hen 1 × male 5 gives ½ medium, ½ low.
Hen 2 × male 1 gives ½ high, ½ medium.
Hen 2 × male 2 gives ½ high, ½ medium.
Hen 2 × male 3 gives ½ high, ½ medium.
Hen 2 × male 4 gives all medium.
Hen 2 × male 5 gives all medium.

What are the probable genotypes for fecundity of these seven birds?

From which of these 10 crosses would you be most likely to get the best males for producing high-laying hens?

42. Note.—White eye in Drosophila is a sex-linked recessive.

In Drosophila, if a white-eyed female is crossed with a red-eyed male and the F_1 allowed to interbreed freely, what will be the appearance of the F_2 as to eye color?

43. In Drosophila, if a homozygous red-eyed female is crossed with a white-eyed male and the F_1 allowed to interbreed freely, what will be the appearance of the F_2 as to eye color?

44. In Drosophila, vestigial wings (v) are recessive to the normal long wings (V), and the gene for this trait is not in the sex chromosome. If a homozygous white, long female is crossed with a homozygous red, vestigial male, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 with each parent type?

45. In Drosophila, two red-eyed long-winged flies when bred together produce the following offspring: females, ¾ red, long; ¼ red, vestigial; males, ⅜ red, long; ⅜ white, long; ⅛ red, vestigial; ⅛ white, vestigial.

What are the genotypes of the parents?

46. In Drosophila, a cross between bar-eyed female and wild-type (round-eyed) produces only bar-eyed male and female in the F_1. Wild-type female crossed with bar-eyed male produces bar female and wild-type male. Explain the inheritance of bar eyes and predict the appearance of the F_2 from each of these crosses.

47. If a white-eyed nondisjunctional female Drosophila, $(Xr)(Xr)Y$, is mated to a red-eyed male, what kinds of offspring may be expected as to sex and eye color?

48. A factor l in Drosophila is recessive, lethal, and sex-linked. If female Ll is crossed with a normal male, what should be the sex ratio of the progeny?

49. In Drosophila vermilion eye color is recessive and sex-linked. In exceptional cases vermilion female crossed with normal male produces, in addition to the usual vermilion male and red-eyed female, a few vermilion female and red male. Explain this result and predict what classes of offspring should appear when the vermilion F_1 females from above are crossed with red-eyed males.

50. In Drosophila yellow body color (y) is sex-linked and recessive to the gray (Y) body of the wild fly.

If a yellow female is crossed with gray male, and (a) if an F_1 female from this cross is mated with her father and (b) an F_1 male mated with his mother, what will be the appearance of the offspring of these last two crosses as to body color?

51. If a hen that undergoes sex reversal, and thus becomes a functional male, produces gametes of the same chromosomal constitution as before (although they are now sperms instead of eggs), what will be the sex of her offspring when she is mated with a normal hen?

52. If such a sex-reversed hen were barred, what would be the appearance of her offspring when bred to a nonbarred hen?

53.* A bald man whose father was not bald marries a nonbald woman whose mother was bald. What are the genotypes of these two people in regard to the factors for baldness and nonbaldness? What kinds of children can they have in regard to these characters?

54.* A nonbald, normal-visioned man marries a nonbald, normal-visioned woman whose father was color-blind and whose mother was bald. What kinds of offspring may they have, and in what proportions?

55.* A nonbald man marries a nonbald woman. They have a son and a daughter. At the age of thirty-five the son becomes bald. What are the chances that the daughter will also become bald because of her genetic constitution?

56.* A red-and-white Ayrshire cow whose mother was mahogany-and-white is bred to a red-and-white Ayrshire bull. If she produces a male calf, what are the chances that it will be mahogany-and-white? If the calf is a female, what are the chances that it will be mahogany-and-white? This is a sex-influenced character.

57.* Outline the breeding procedure necessary to establish a homozygous mahogany-and-white Ayrshire herd.

58.* Outline the breeding procedure necessary to establish a homozygous red-and-white Ayrshire herd.

59. NOTE.—In sheep, white fleece (W) is dominant over black (w); and the horned condition (h) is dominant over the hornless (H) in males but recessive in females.

If a homozygous horned, white ram is bred to a homozygous hornless, black ewe, what will be the appearance of the F_1 and F_2 as to color and horns?

60. A horned, black ram bred to a hornless, white ewe has the following offspring: Of the males, ¼ are horned, white; ¼ horned, black; ¼ hornless, white; and ¼ hornless, black. Of the females, ½ are hornless, black and ½ hornless, white. What are the genotypes of the parents?

61.* How many times in families of five would you expect four boys and a girl? Four girls and a boy? Five girls?

62.* In a certain family there are six girls. What are the chances of the next child being a boy?

63.* In human beings, deaf-mutism may be the result of the homozygous state of either or both of two recessive factors d and e. Normal hearing results only when both dominants D and E are present. When both parents are $Dd\ Ee$, how many times in families of two would you expect two deaf children?

64.* Where both parents are $DdEe$, how many times in families of four would you expect three normal children and one deaf child?

65.* Two normal parents produce an albino son. What are the chances that their next child will be a normal girl?

66.* In Shorthorn cattle, the factors for red and white are alleles but neither is dominant, the heterozygous condition resulting in roan. Twins are sometimes born in cattle. If twins are born in crosses between red bulls and roan cows, how often should both twins be roan?

67.* In poultry, feathered shanks are the result of either or both of the dominant factors F and S. Unfeathered shanks are the result of the double recessive condition.

In crosses where both parents are *Ff Ss*, how many times in families of three offspring would all be expected to have feathered shanks? All three unfeathered shanks?

68.* If one parent were *Ff Ss* and the other *ff ss*, how many times in families of four offspring would you expect one feathered-shank bird and three unfeathered-shanked birds?

69.* In poultry, the factors for black and for splashed-white are alleles but neither is dominant, the heterozygous condition resulting in blue (the Blue Andalusian). A pair of Blue Andalusians are mated, and the female lays two eggs. What are the chances that both eggs will hatch out Blue Andalusians?

70.* If three eggs are laid by the bird mentioned in Prob. 69, what are the chances that all three eggs will hatch out Blue Andalusians?

CHAPTER XIV

THE PRINCIPLES OF HEREDITY (*Continued*)

Thus far we have studied various types of inheritance that behave as if certain characters were dependent on one pair of genes. Sometimes these genes were in an autosomal chromosome, sometimes in a sex chromosome, sometimes the gene was a dominant or a recessive lethal, sometimes the manifestation of the character was influenced by the sex of the individual. We also discovered that the gene may have more than just two alternative forms, that there may be three or many more genes in a series of multiple alleles.

In addition, we have studied the behavior of two genes simultaneously, both in cases where each pair of genes was responsible for the production of a separate character and those in which the two pairs of genes acted on only one character. In the latter cases, we met many exceptions to the general dihybrid 9:3:3:1 ratio due to various types of epistasis, and we also learned that lack of dominance in one or both pairs of genes can change this ratio. If, however, each of two pairs of genes causes the development of a certain separate character, or in some cases (*e.g.*, comb pattern in poultry) both act on the same character, if there is dominance between the members of each pair of genes, and if the pairs of genes are located in different chromosomes, then the F_2 will give the usual 9:3:3:1 ratio. If instead of mating two F_1's (*Aa Bb*) to get the F_2 we made what is termed the *backcross* by mating an F_1 (*Aa Bb*) to the double recessive (*aa bb*), then we would get equal numbers of four different phenotypic types according to the following diagram.

F_1 (*Aa Bb*) germ cells....................	*AB*	*Ab*	*aB*	*ab*
Double-recessive (*aa bb*) germ cells *ab*......	*Aa Bb*	*Aa bb*	*aa Bb*	*aa bb*

Because each chromosome consists of scores or hundreds of genes, it is logical to suppose that we might sometimes be dealing with two pairs of genes that are located in the same chromosome. In such a case the genes would not assort independently, although the chromosomes would. Genes located in the same chromosome show varying degrees of linkage.

Linkage.—In working with sweet peas in 1906, Bateson and Punnett made a cross involving purple flowers and long pollen grain in one parent and red flowers and round pollen grains in the other. Because crosses of purple and red had given a 3:1 ratio in the F_2 (purple being dominant) and crosses of long and round pollen grains had likewise given a 3:1 ratio in the F_2 (long pollen grains being dominant), it was expected that the F_2 of the purple, long crossed with red, round would thus give a ratio of 9 purple, long:3 purple, round:3 red, long:1 red, round. Such, however, was not the case, for out of 6,952 F_2 flowers 4,831 (instead of the expected 3,910.5) were purple, long; 390 (instead of 1,303.5) were purple, round; 393 (instead of 1,303.5) were red, long; and 1,338 (instead of 434.5) were red, round. Combinations of the two genes that had gone into the hybrid together (purple and long from one parent and red and round from the other) were much too numerous in the F_2. Actually there was a total of 6,169 of these two classes where only 4,345 had been expected. Bateson and Punnett called this feature *coupling*, and its opposite, where a dominant and a recessive were supplied by each parent (purple and round and red and long) and still too few of the new types appeared in the F_2, *repulsion*, these of course being different aspects of the same problem.

Facts like these stood out as exceptions to Mendelian inheritance until 1910, when Morgan and his coworkers at Columbia University discovered the basis for these phenomena from their work with Drosophila and coined the term that describes them, *linkage*. If two genes with recognizable end products are in the same chromosome, they will, of course, have more or less tendency to be inherited together.

In Drosophila, if a cross between a wild-type (gray) body color with long wings and a black body color with vestigial wings is made, the F_1 all have gray bodies and long wings, for these patterns are dominant to black and vestigial. If a male of this F_1 hybrid generation is mated to a black, vestigial female, we would expect to get some gray, long; gray, vestigial; black, long; and black, vestigial offspring. If the genes for these characters were in different chromosomes, we would expect equal numbers of the above classes. If they were in the same chromosome, we would expect to get more than 50 per cent of the grandparental types and less than 50 per cent of the new combinations. Actually, in this case, we get 100 per cent of the grandparental types and 0 per cent of new combinations. In other words, these genes remain completely linked when tested by this backcross.

The backcross to the double recessive is used to determine the sort of germ cells that the F_1 dihybrid is producing, because there is nothing in the double recessive to hide what is going on in the dihybrid.

The usual system of notation when dealing with linkage problems is to use the plus sign for wild-type genes (usually dominant) and a letter for the mutated gene. In the above case, the notation applicable with independently assorting genes, *e.g.*, *GG LL* for a gray-bodied long-winged fly cannot be used because we know from the genetic behavior that the genes for gray body and long wings are in the same chromosome and, therefore, belong together. We could write the genetic make-up of such a fly (*GL*)(*GL*), but it is more convenient to write it ++/++ (plus sign standing for the wild-type genes).

Thus a diagram of the above cross would be written

$$P_1 \frac{++}{++} \times \frac{gl}{gl}$$

gray, long   black, vestigial

$$F_1 \frac{++}{gl}$$

gray, long male

and the backcross of an F_1 male to the double recessive

$$\frac{++}{gl} \times \frac{gl}{gl} = \frac{++}{gl} \text{ and } \frac{gl}{gl}$$

gray, long 50%   black, vestigial 50%

Crossing Over.—We have just seen that the backcross of a dihybrid gray-bodied long-winged male, $++/gl$, to a double-recessive black, vestigial female, gl/gl, gives only two sorts of offspring, ½ of them being gray, long, $++/gl$, and ½ black, vestigial, gl/gl, because the linkage of the *G* and the *L* genes and the *g* and *l* genes in the dihybrid male was complete.

However, if we take a dihybrid female with gray body and long wings, $++/gl$, and mate her to a double-recessive male, gl/gl, we will secure four kinds of offspring instead of two, *viz.*, gray, long; black, vestigial; black, long; and gray, vestigial. The reason for this evidently is that there has been crossing over between the loci for body color and length of wings, as illustrated in Fig. 102. The end result is that the genes *G* and *L* and *g* and *l* in this female dihybrid usually stay together but occasionally through crossing over get into the new combinations of *G* and *l* and *g* and *L*, or $+l$ and $g+$.

The following schematic diagram shows the manner in which the new gene combinations are formed. We have learned earlier that the pairs of homologous chromosomes come to lie side by side during the early stages of germ-cell production in the process called *synapsis*. In the early stages

of synapsis, each member of each homologous pair of chromosomes reproduces itself so that the pair of homologous chromosomes becomes two pairs of closely associated sister chromatids. Crossing over, or the equal interchange of blocks of genes in sections, apparently takes place between two nonsister chromatids after the two chromosomes have become bundles of four chromatids. In other words, crossing over involves two chromatids rather than two chromosomes.

In mitosis, or somatic cell division, the chromosomes shorten and thicken and arrange themselves in the equatorial plate (prophase). They next split or reproduce themselves (metaphase) so that each chromosome is now double. The members of each exactly similar doublet now start to move to opposite poles of the cell (anaphase). Finally the migration is complete (telophase), and the cell wall constricts, forming two cells exactly like the parent cell. In other words, in mitosis the chromosomes appear in the diploid number of paired threads. In meiosis, or germ-cell production, however, they appear as the haploid number of paired threads. This latter feature is due to synapsis, or conjugation of the homologous chromosomes, which is specific in that all the allelic genes are attracted to each other and come to lie side by side in a regionally specific fashion—gene *A* with *A* or *a*, gene *B* with *B* or *b*, etc.

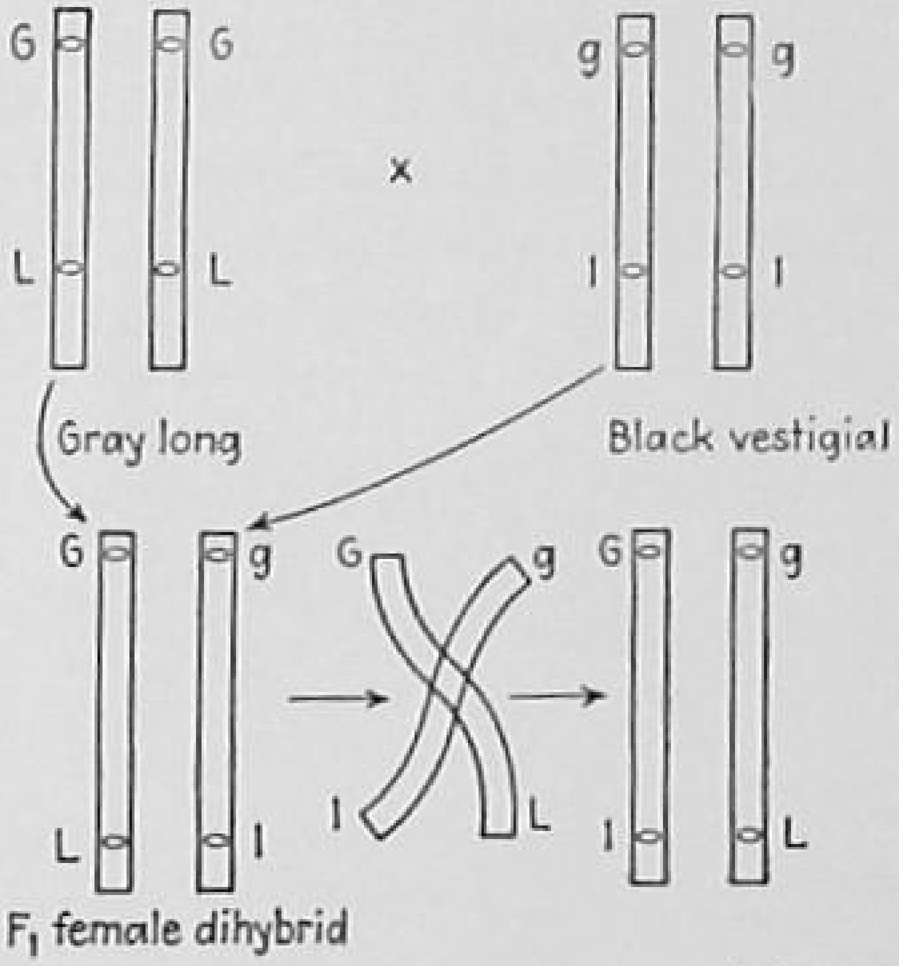

FIG. 102.—Schematic crossing over between loci for body color and wing length.

In the earliest prophase stage of meiosis, the chromosomes are strung out into long unpaired threads in the diploid number (leptotene stage). They next are attracted into homologous pairs (zygotene stage or synapsis). They next split or reproduce into bundles of four chromatids, two from each chromosome (pachytene stage). Finally in the last stages of prophase (diplotene, diakinesis) they show chiasma as the paired chromatids begin to open out. During these four stages the chromosomes have been shortening and thickening.

Each group of two sister chromatids is held together by an unstaining portion of the chromosome called a *centromere*. These centromeres appear to repel each other, and, as the bundle of four chromatids begins to be drawn apart by the retreating centromeres pulling each pair of

two sister chromatids (formed from one chromosome) to opposite poles along the plane of conjugation, two of the nonsister chromatids often appear to be crossed, these crosses being chiasmata (singular, chiasma). These crosses are apparently due to one of a pair of sister chromatids breaking at the original point of the chiasma and becoming attached to the remaining portion of one of the members of the other pair of sister chromatids and the remaining portions of the two broken chromatids themselves uniting into a whole chromatid as diagramed in Fig. 103.

It is obvious that, if crossing over took place in every cell containing the chromosomes diagramed in Fig. 103, the result would be equal numbers of *GL*, *Gl*, *gL*, and *gl* germ cells and would amount to 50 per cent of crossing over. Such a situation could not be differentiated genetically from independent assortment. Actually such a situation is not known. The greatest amount of crossing over yet found amounts to about 48 per cent, the least, 0 per cent as illustrated earlier in the Drosophila cross

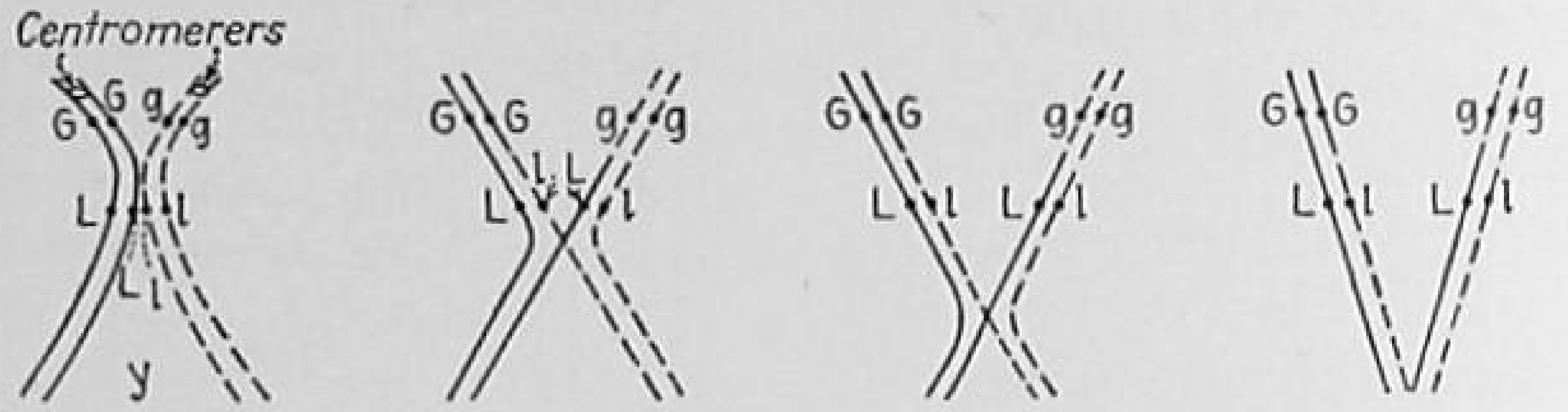

FIG. 103.—Diagram of chiasma at *x* with resulting crossing over between the genes *G* and *L*, thus resulting in the production of germ cells containing *GL*, *Gl*, *gL*, and *gl* genes.

involving the use of a *GL*/*gl* male on *gl*/*gl* females, from which only *GL*/*gl* and *gl*/*gl* offspring resulted.

It has been found that the number of chiasmata at any given region is about twice the amount of crossing over. Again referring to Fig. 103, if we were considering 100 sets of these chromosomes and found no chiasma in 80 of them, all these resulting germ cells would contain the original combinations *GL* and *gl*. The other 20 per cent would show chiasma, but 25 per cent of the resulting germ cells would contain *GL* and 25 per cent *gl*, whereas the other 50 per cent (of the 20) would be *Gl* and *gL* (25 per cent of each). In other words, there were 20 per cent of chiasma to but 10 per cent of crossovers. Crossing over takes place between only two of the four chromatids, in something less than 100 per cent of the possible cases and always between two nonsister chromatids.

Crossover percentage, of course, is obtained by dividing the total number of crossovers by the total population. Morgan gives,[1] among others, the following instances of crossing over in Drosophila:

[1] MORGAN, T. H., "The Physical Basis of Heredity," pp. 87–88, J. B. Lippincott Company, Philadelphia, 1919.

When a black fly with vestigial wings is crossed to a wild-type ("gray") fly with long wings the offspring are, as we have already seen, gray, long. If one of the F_1 females is back-crossed to a black vestigial male there are four kinds of offspring produced; *viz.*, the two original combinations, black vestigial, and gray long; and in addition two recombinations of these; *viz.*, black long, and gray vestigial. The two latter classes are called the crossover classes, or, more briefly, crossovers. The percentage of crossovers is definite for a given stock, of a given age, and under given environmental conditions. In this case the percentages are as follows:

Non-crossovers		Crossovers	
Black vestigial	Gray long	Black long	Gray vestigial
41.5 per cent	41.5 per cent	8.5 per cent	8.5 per cent
83 per cent		17 per cent	

If a pair of chromosomes in the F_1 fly is represented as carrying the genes of the characters here involved, one member of such a pair carries both a gene for black and a gene for vestigial; the homologous member of the pair of chromosomes carries both of the normal alleles; *viz.*, a gene for gray and a gene for long wings. When crossing over takes place so that a gene for black goes over into the other chromosome, the converse phenomenon takes place, a gene for gray goes over into the chromosome that gave up its black gene. It is the constancy of this interchange that makes the phenomenon reducible to exact mechanical treatment.

Using the usual notation, we would have, in this last cross of an F_1 female from a gray, long crossed with black, vestigial mated back to a double-recessive black, vestigial, the results indicated in the following diagram.

$\frac{++}{++}$ gray, long × $\frac{gl}{gl}$ black, vestigial

F_1, $\frac{++}{gl}$ female × $\frac{gl}{gl}$ = backcross

F_1 germ cells plus double-recessive germ cell, $\frac{++}{gl}$ gray, long; $\frac{gl}{gl}$ black, vestigial; $\frac{g+}{gl}$ black, long; $\frac{+l}{gl}$ gray, vestigial

numbers, 41.5% 41.5% (noncrossovers) 8.5% 8.5% (crossovers)

Strength of linkage = 83% Crossover percentage = 17%

The reduction in the number of chromosomes in the germ cells is accomplished by the two meiotic divisions. In the first, the chromosomes after synapsing become double through reproducing or splitting, each chromosome forming two chromatids closely applied to each other. This bundle of four chromatids then separates along the plane of conjugation

(with possible crossing over), two closely applied sister chromatids passing to each secondary spermatocyte or oöcyte, this division being spoken of as the *heterotypic* division. These secondary spermatocytes then quickly go through another cell division, at which time one member of each pair of sister chromatids goes to each resulting cell. This is known as the *homotypic* division, and through these two rapid cell divisions the number of chromosomes is both reduced to one-half and the possibility of recombination of blocks of genes from the two parents provided.

It is readily seen in Fig. 103 that if another pair of genes *C* and *c* were located near the bottom of the chromosomes, and if another chiasma appeared at point *y*, we might have a repetition of the above-described

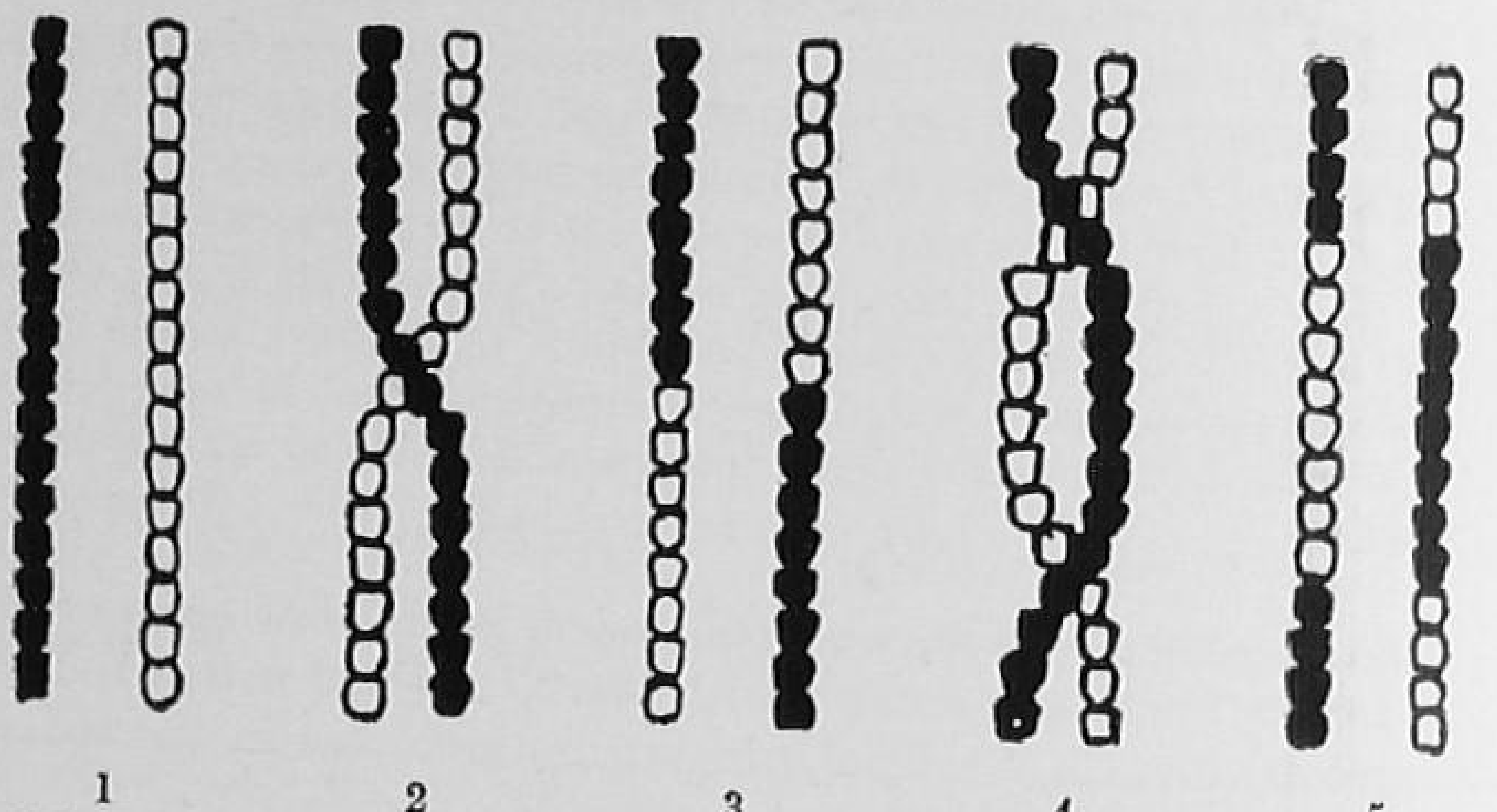

FIG. 104.—Diagrammatic representation of single crossing over between homologous chromosomes 1–3; and double crossing over 4 and 5.

process with the result that genes *GlC* and *gLc* might be located in two chromatids. This would be a case of double crossing over, and, although two crossings over had occurred between *G* and *C*, they would still be in the same chromatid, which makes it appear genetically that no crossing over had occurred between them. Thus each case of double crossing over hides two actual crossovers, and allowance must be made for this fact in ascertaining crossover percentages involving situations of this sort.

If, in any cross involving genes located in the same chromosome and thus showing various degrees of linkage, the crossover percentage is found to be 20 per cent, the same fact can be stated by saying that the strength of the linkage is 80 per cent.

Under standard conditions the percentage of crossing over remains constant between any two pairs of genes. However, experimental work has

shown that a variety of internal and external conditions may affect this rate. Among these influences are sex, no crossing over in the male of Drosophila normally, although this can be induced in the autosomes by X-ray treatment; chromosomal aberrations such as the inversion of a section of the chromosome, translocations, etc., as well as gene mutations; and, in addition, age and temperatures.

Much of the study of crossing over is made by means of the back-cross. However, the F_2 is sometimes used, and mathematical formulas have been devised for the interpretation of the results.

If we were dealing with a case that showed 20 per cent of crossing over between two genes *AB* and *ab*, then the F_2 ratios could be found by the usual checkerboard arrangements, as illustrated in Fig. 105.

	4 *AB* (40%)	1 *Ab* (10%)	1 *aB* (10%)	4 *ab* (40%)
4 *AB* (40%)	16 (*AB*) (*AB*)	4 (*Ab*) (*AB*)	4 (*aB*) (*AB*)	16 (*ab*) (*AB*)
1 *Ab* (10%)	4 (*AB*) (*Ab*)	1 (*Ab*) (*Ab*)	1 (*aB*) (*Ab*)	4 (*ab*) (*Ab*)
1 *aB* (10%)	4 (*AB*) (*aB*)	1 (*Ab*) (*aB*)	1 (*aB*) (*aB*)	4 (*ab*) (*aB*)
4 *ab* (40%)	16 (*AB*) (*ab*)	4 (*Ab*) (*ab*)	4 (*aB*) (*ab*)	16 (*ab*) (*ab*)

FIG. 105.—Checkerboard showing the expected composition of the F_2 from a cross between individuals differing in two linked genes which show 20 per cent of crossing over. The F_2 ratio is 66 *AB*:9 *Ab*:9*aB*:16 *ab*.

Cytological Proof of Genetic Crossing Over.—We have looked at the evidence that crossing over takes place. We saw that a cross involving a gray-bodied long-winged female Drosophila of genetic constitution ++/*gl* and a double recessive male *gl*/*gl* gave four types of offspring, ++/*gl*, *gl*/*gl*, +*l*/*gl*, and *g*+/*gl*, in the proportion of 41.5 per cent gray, long; 41.5 per cent black, vestigial; 8.5 per cent gray, vestigial; and 8.5 per cent black, long owing to the supposed fact that crossing over between these points occurred in 17 per cent of the germ cells of the female. To clinch the matter or to establish this supposed fact, we need cytological evidence that it actually occurs.

This is difficult to get because the chromosomes and their various parts generally lack distinguishing marks. However, Stern, working with Drosophila, and Creighton and McClintock, working with maize, have furnished this proof. Stern found a strain of Drosophila in which a portion of the Y chromosome had been broken off and become attached to an

X chromosome. He found another strain in which a portion of an X chromosome had been broken off and become attached to the IV chromosome. A cross between these two races gave him a race in which both the X chromosomes had distinguishing marks and could be differentiated

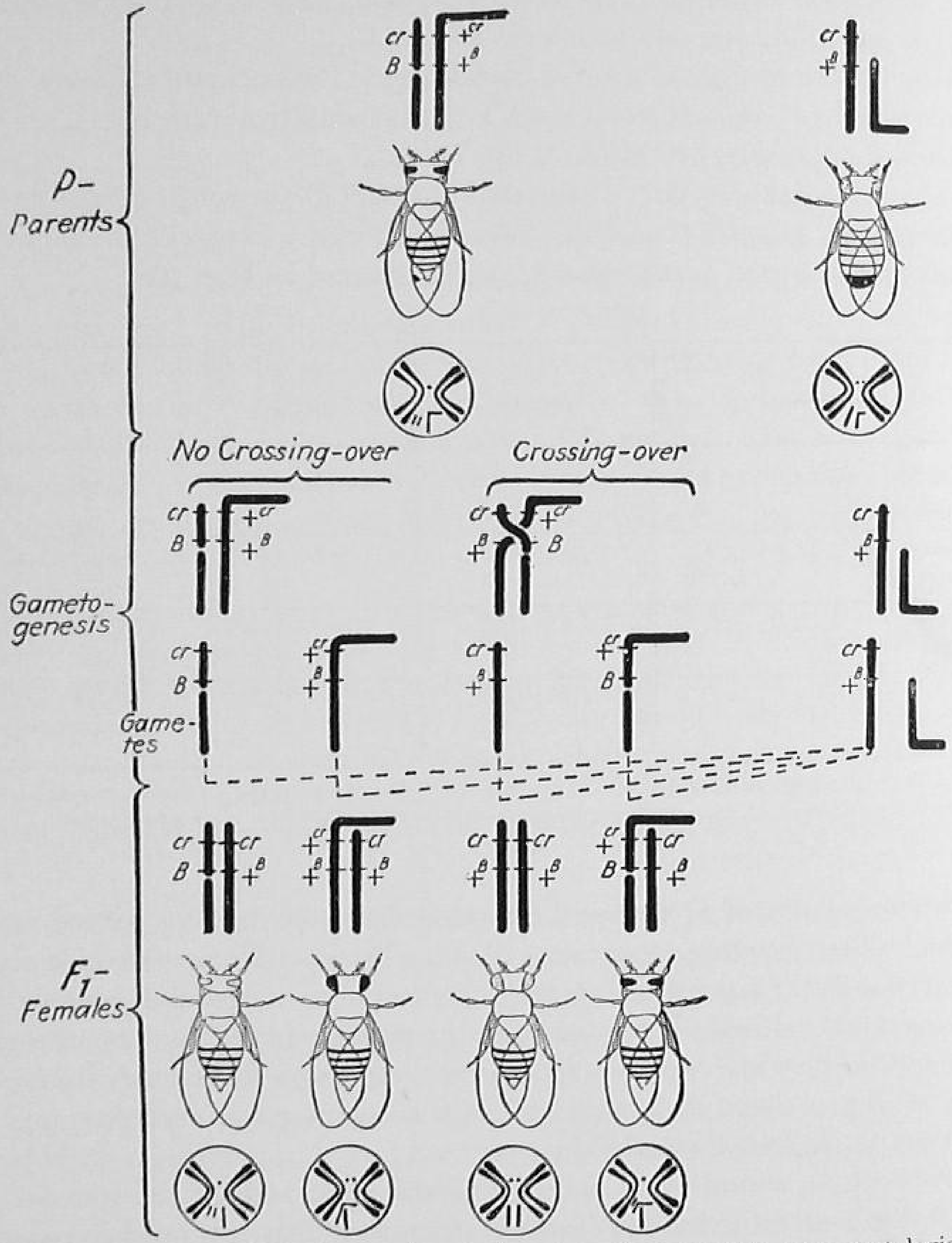

FIG. 106.—Diagram of Stern's experiment demonstrating crossing over cystologically. See text for details. (*From Stern, after Sinnott and Dunn.*)

microscopically from all ordinary X chromosomes. Stern now made up a stock of flies that had the genes for carnation eye color and the bar eye pattern in the upper end of the broken X chromosome and the gene for red eyes and round eye pattern in the upper end of the X chromosome

with the attached piece of the Y chromosome, the red eye and the bar pattern being dominants.

Red-eyed and bar-eyed females of the genetic constitution $crB^*/++$ were then mated to males of the genetic constitution cr + *i.e.*, round eyes of carnation color in their only X chromosome (round being the wild-type eye shape but recessive to the mutant bar pattern). From this cross we would expect four types of females if crossing over between the two pairs of genes for eye color and eye shape had occurred. Stern secured the expected four classes of females, *viz.*, carnation, bar; red, round; carnation, round; and red, bar. The first class should have had the broken X chromosome plus a normal X from the male. The second should have had one X chromosome with the attached piece of the Y chromosome plus a normal X from the male. The third should have had two normal X chromosomes, one from the male and the other as the result of crossing over between the two marked chromosomes of the female at a point between the two genes being considered, whereas the fourth should have had one normal X from the male plus a broken X chromosome with the piece of the Y chromosome attached to one of the pieces.[1]

These are the results which should obtain if there had been an interchange between the two X chromosomes of the mother at a point near the upper end of the X and between the locations of the *cr* and *B* genes. Of the F_1 female flies, 364 were tested by Stern and in all but 5 (and these presumably the result of experimental error) there was a complete correspondence between the genetic and the cytological facts. In other words, genetic crossing over was proved to be accompanied by cytological crossing over, an actual exchange of material between homologous chromosomes.

Linear Order of Genes.—We have seen in the two preceding sections that blocks of genes or sections of homologous chromosomes sometimes interchange their positions in the chromosomes so that new combinations of genes can be formed, even though the genes controlling these characters are not in separate chromosome pairs. We learned too that the percentage of the crossing over can be easily ascertained by dividing the total crossovers by the total population.

Now, if we assume that the chromatids are as likely to form chiasma, with resulting interchange, at one point as at another, then the percentage of crossing over can be taken as the measure of the distance between the genes being studied. For, if crossing over is as apt to occur at one point as at another then there will be less likelihood of a break occurring

* The bar-eyed mutation behaves as a dominant.

[1] SINNOTT, EDMUND N., and DUNN, C., "Principles of Genetics," 3d ed., p. 222, McGraw-Hill Book Company, Inc., New York, 1939.

between two closely spaced genes than between two more widely spaced ones.

For example, it has been found by Morgan and his coworkers that the crossover percentage between the genes for yellow body color and white eyes is 1.5 per cent and that between white eyes and bifid wings is 5.5 per cent. Further crosses involving yellow body color and bifid wings gave a crossover value of 7.0 per cent. Now the simplest explanation of these results is that these genes lie in a straight line, for no other geometric configuration would explain the results equally well. If, therefore, we know that three genes are in the same chromosome, because they all show linkage, and breeding results show that the crossover percentage between genes *A* and *B* is 5 per cent and that between *B* and *C* is 10 per cent, then we can predict that the crossover percentage between *A* and *C* will be either 15 per cent or 5 per cent. It will be either the sum or the difference of the two already ascertained crossover percentages, depending on which side of *B* gene *C* happens to lie.

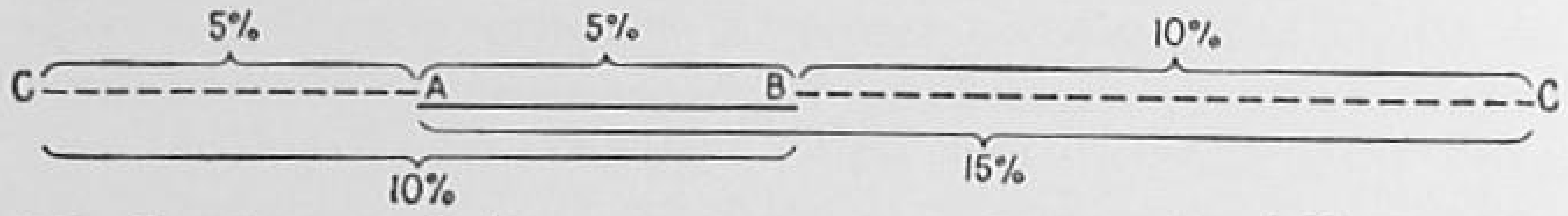

FIG. 107.—Locating gene *C* when crossover percentage between *A* and *B* is 5 per cent and that between *B* and *C* is 10 per cent.

The above procedure in locating genes in a line on the basis of crossover percentages holds good only when we are dealing with genes lying fairly close together, for, if they are far removed from each other, there may be double or multiple crossing over that would becloud the actual situation. On the basis of crossover percentages, some of the chromosomes in Drosophila are over 100 units long, and obviously we could not have more than 50 per cent of crossing over, in fact, never get as much as 50 per cent.

Chromosome Maps.—By means of linkage and translocation studies, genes can be located in specific chromosomes; and, on the assumption that crossing over is as likely to occur at one point as at another in the chromosome, they can be located at definite points in the chromosome. The unit of distance is taken as 1 per cent of crossing over, so that, if gene *B* shows 5 per cent of crossing over with gene *A*, it is placed 5 units away from *A*. Obviously genes that are 100 units removed from each other do not show 100 per cent of crossing over. Thus genes "star" and "speck" in the second chromosome in *D. melanogaster* are 105 units apart on the maps (Fig. 108) but show a crossover value of only 48.7 per cent because of double and multiple crossing over. These long distances between genes are arrived at by summating the crossover percentages of genes lying fairly close together between the widely separated genes.

The recent work with the giant salivary-gland chromosomes of Drosophila has afforded the opportunity of making cytological maps of the bands that are or contain actual genes. The correspondence between the order of the genes in the genetic or crossover maps and the cytological maps is perfect. However, there appear to be discrepancies in the actual distances secured by the two methods.[1]

The discrepancies are greatest at the centers of the two large autosomes and at the right or "bobbed" end of the X chromosome. In these regions one crossover unit corresponds to a relatively much greater distance on the physical chromosome than in other regions. It happens that these are the regions of spindle-fiber attachment, and it is evident that in these places the frequency of crossing over per unit of chromosome length is low. Moreover it appears that no less than one-third of the whole length of the X chromosome, at the spindle-fiber end, is inert in the sense of containing practically no known gene loci (only bobbed near the end) and very little crossing over occurs in it. The crossover distance from the locus of carnation (*cr*) to the end is only about 7 units (10 per cent of the genetic length), yet this region comprises over 30 per cent of the metaphase chromosome. Near the spindle-fiber attachments of the II and III chromosomes there are also inert regions. It seems clear then that the unit of measure in the crossover maps is a variable one and that the amount of crossing over in any region is related to its proximity to the spindle-fiber attachment and to other regional peculiarities in the chromosomes.

By studying various inversions, translocations, deficiencies, and duplications in the salivary chromosomes of flies with known mutant genes, Painter, Bridges, Demerec, and others have been able to specify the physical location of a number of genes. A recent salivary map of the X chromosome, compared with the crossover map, is shown in Fig. 111. The gene order is the same in both maps, and the relations between crossover values and physical distance vary as they do when the metaphase map is used. The inert region of the X appears in the salivary chromosome only as a few faint bands at the spindle-fiber end; and probably consists, as does the Y chromosome, chiefly of heterochromatin, that is, chromatin which does not respond to the chromatin stains used. Thus those portions that contain few or no mutant genes are also structurally different from the gene-bearing portions.

In a few cases individual gene loci have been identified with individual bands, suggesting that these are or contain the actual genes.

The chromosome map of Drosophila is the most complete at present, but that of the 10 chromosome pairs in corn is growing rapidly. These maps have grown out of thousands of breeding experiments and must be acknowledged as among the most ingenious things the mind of man has ever contrived.

[1] *Ibid.*, pp. 232–233.

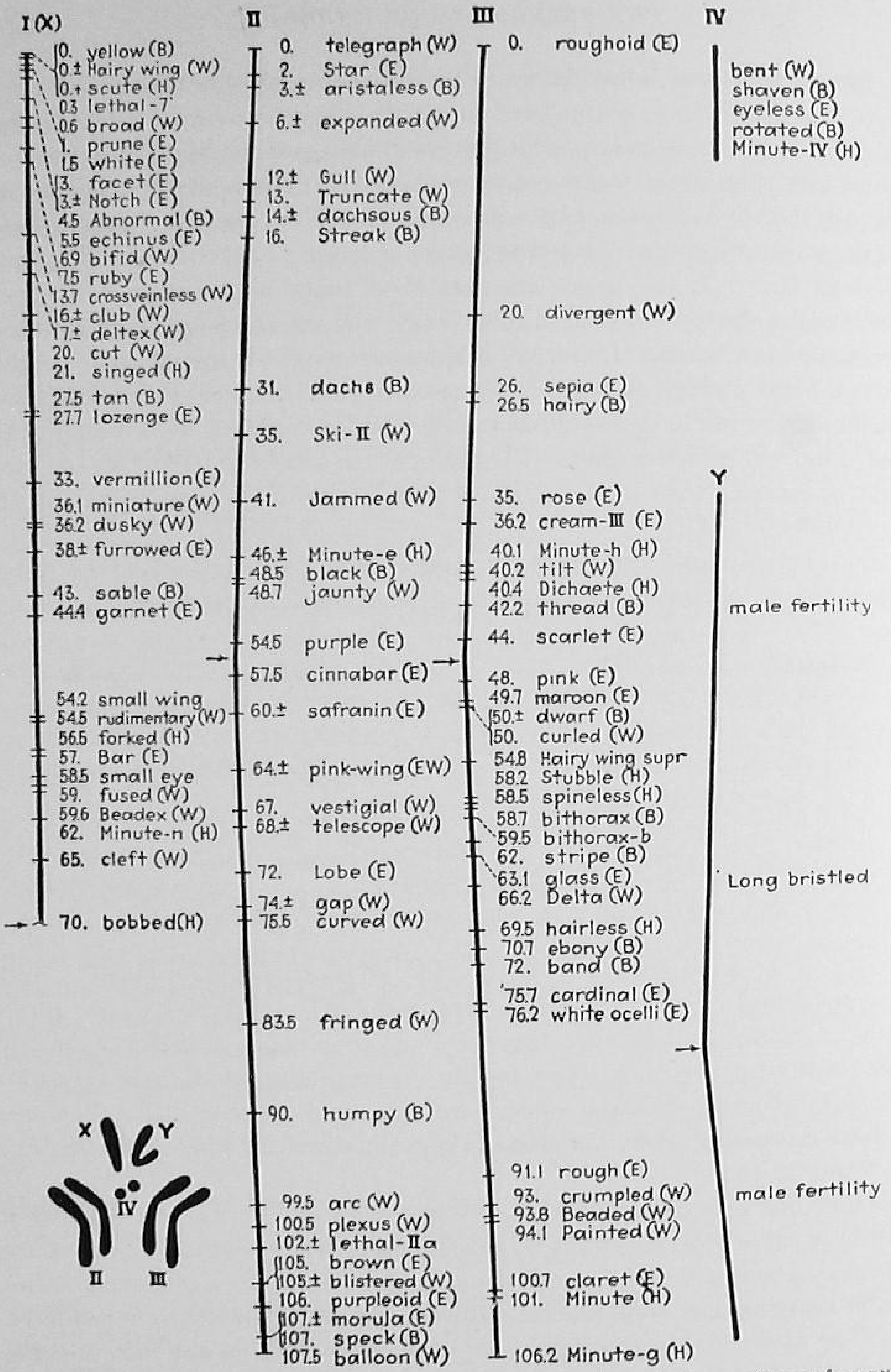

FIG. 108.—Linkage map for *Drosophila melanogaster*, showing relative positions of many of the known genes in the chromosomes as determined genetically. The letters in parentheses indicate the portion of the fly in which the characters appear: *B*, body, *E*, eye; *H*, hairs; *W*, wings. The arrows indicate positions of spindle-attachment regions. In the *Y*-chromosome, "Long bristled," which is the normal allelomorph of "bobbed," and the two factors for male sterility have not been precisely located. In chromosome IV the genes are all very closely linked. [*From Sharp, adapted from Morgan, Sturtevant, and Bridges* (1925) *and Stern* (1929).]

Interference and Coincidence.—We have seen that crossing over may take place between two nonsister chromatids at synapsis, which gives rise to recombinations of genes, although they are located in the same chromosome, and that these crossover percentages are taken as the measure of the distance between the genes in constructing chromosome maps based on the assumption that the crossing over is as apt to take place at one spot as at another. If two genes are very close together in the chromosome, they might show complete linkage, *i.e.*, the chromosome might never break between them. Likewise, if genes are very far apart, there might be two breaks, or crossovers, between them, so that in spite of this they would still be in the same chromosome and appear as if no crossing over had occurred between them. Therefore, the maps are built up on the basis of crossing over between genes that lie relatively close together, up to 10 units.

With three pairs of genes *A*, *B*, and *C* that were located in the same chromosome we might get the sorts of combinations shown in Fig. 109.

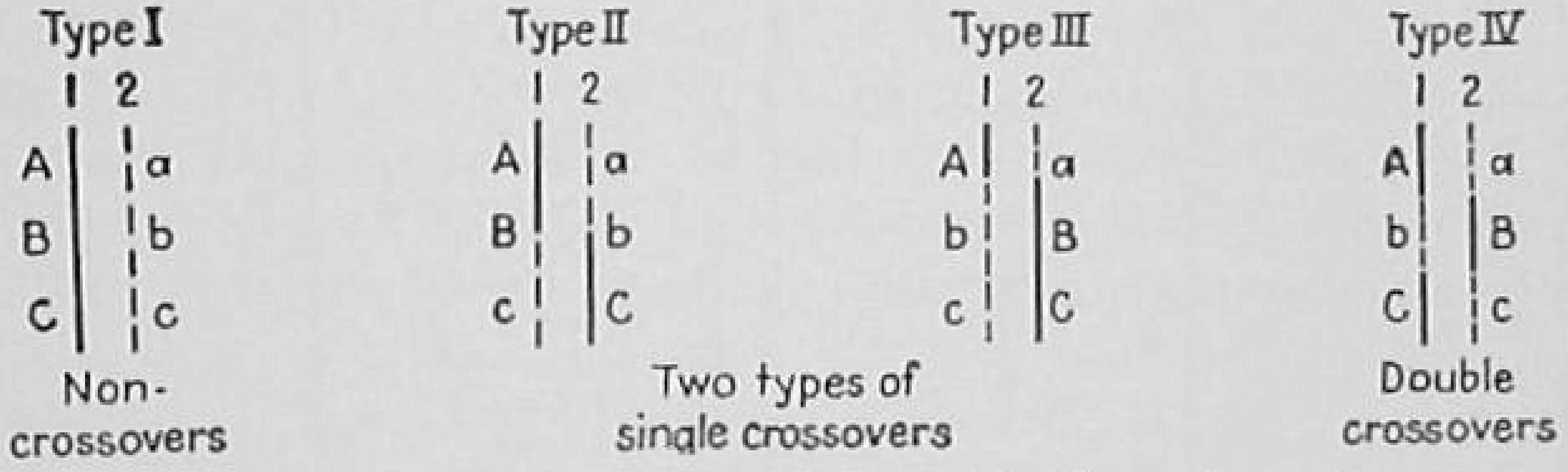

FIG. 109.—Diagram showing single and double crossing over.

Now, if we were studying the linkage relations between genes *A* and *C*, types I and IV above would appear similar genetically because genes *A* and *C* and *a* and *c* occur together. It is evident, therefore, that, if genes are relatively far apart in the chromosome, there will be more actual cytological crossing over than is apparent genetically, because of double crossing over, and that allowance must be made for this fact mathematically.

If breeding experiments had shown genes *A* and *B* (Fig. 109) to have a crossover value of 20 per cent and genes *B* and *C* 10 per cent, then we would expect that genes *A* and *C* would show a crossover value of 30 per cent if no double crossing over took place. However, genes *A* and *C* are far enough apart so that double crossing over is possible and would infrequently occur. Such double crossing over would still leave genes *A* and *C* and *a* and *c* in the same chromosomes, the first marked by containing gene *b*, the second by containing gene *B*, so that each double crossing over hides or masks two actual crossovers. If, then, in the backcross we

secured 71 per cent of type I, noncrossovers; 9 per cent of type II and 19 per cent of type III, single crossovers; between *A* and *C*; and 1 per cent of type IV, double crossovers, between *A* and *C*, we would have to add two times the 1 per cent, or 2 per cent, to the 28 per cent of single crossing over between *B* and *C* and *A* and *B* to get the actual amount of crossing over, or 30 per cent. Thus, when genes lie relatively far apart in the chromosomes, the apparent amount of crossing over will be less than the actual amount because of double crossing over.

Now, if the break between *A* and *B* occurs in 20 per cent of the cases and between *B* and *C* in 10 per cent of the cases, and if these breaks are entirely independent of each other, then they should both occur 10 × 20, or in 2 per cent of the cases, for the likelihood of two independent events occurring at the same time is the product of the likelihood of each occurring separately. We saw, however, that the break occurred in both places in only 1 per cent of the cases.

Varying degrees of less than expected double crossing over are usually secured. That is to say, these breakings and crossings over in different regions of the chromosomes are not independent events but are influenced by each other so that if a break occurs between any two given genes, *e.g.*, *A* and *B*, the likelihood of a break occurring between *B* and *C* is somewhat reduced. A break at a given point in a chromosome protects the contiguous region from any breakage. This principle is known as *interference*. If three genes lie very close together in a chromosome, we may get breaks between the first and second or between the second and third pairs but never between both the first and second and the second and third simultaneously, *i.e.*, no double crossing over. Such a situation holds, for example, between the mutant genes yellow (body), white (eyes), and bifid (wings) in the X chromosome of Drosophila, which show 1.5 per cent of crossing over between yellow and white and 5.5 per cent of crossing over between white and bifid. Here, if the events were independent, we would expect both to happen in 1.5 × 5.5 or 0.08 per cent of the cases. Interference is sometimes expressed as a coefficient of coincidence, which is secured by dividing the actual proportion of double crossovers by the expected proportion. In the above case we would have

$$\frac{0}{0.0008} = 0, \text{ the coincidence value}$$

A coincidence value of 0 means that interference is complete. Likewise a coincidence value of 1 would mean no interference or complete independence of crossing over between the two regions of the chromosome. In the other example cited earlier in this section, the actual pro-

portion of double crossing over was 1 per cent, the expected 2 per cent thus giving a coincidence value of 0.5.

Limitation of the Linkage Groups.—We have now discussed six Mendelian principles, *viz.*, segregation, independent assortment, linkage, crossing over, linear order of the genes, and interference. There is one final principle to be added to this list known as *limitation of the linkage groups.* In *Drosophila melanogaster*, four linkage groups are known; *viz.*, a large group of sex-linked genes located in the I chromosome, two large groups of autosomal genes in the large II and III chromosome pairs, and a small group of genes located in the small IV chromosome pair.

TABLE 22.—LINKAGE-GROUP RELATIONS

Species	Chromosome pairs	Known linkage groups
Drosophila melanogaster	4	4
D. willistoni	3	3
D. pseudobscuria	5	5
D. virilis	6	6
Corn	10	10
Pea	7	7
Tomato	12	10
Morning glory	15	12
Mouse	20	15
Rabbit	22	11

Each new mutant in Drosophila has proved to be linked to other genes in one or another of these four pairs of chromosomes. Such findings are of course basic to the validity of the fundamental theory of chromosomal inheritance. Obviously, if a fifth group of genes were ever discovered in *D. melanogaster*, the whole theory of chromosomes and genes would have to be entirely revamped or discarded.

Table 22 shows the linkage-group relations in several species.

Application to Farm Animals.—The foregoing principles of inheritance have been worked out from breeding experiments with plants, insects, or small laboratory animals. These species reproduce rapidly, have large numbers of offspring, and are inexpensive to grow. None of these three features holds with our larger farm animals.

The principles have been and are being used, however, to explain various types of inheritance in the larger farm mammals. Up to the present, no contradictions to established principles have been found, although in many instances the principles must be applied in general rather than in specific ways. Unfortunately in the higher animals we

have large numbers of chromosome pairs and small numbers of offspring. This, together with the fact that the environment is so diverse and its influence in many cases so great, leads to many difficulties in applying the known principles in any detailed manner.

A knowledge of basic principles and an assurance that they hold for all living forms gives the animal breeder a firm foundation on which to base his breeding operations. At least the main routes toward his goal of beautiful form and efficient function are now more clearly delineated and should prevent his choosing an entirely wrong road or taking too many expensive and time-wasting detours.

Genes and Development.—It will be recalled that in Chap. XI we listed three problems of genetics. One of these had to do with the actual nature of the genes, about which very little is known at the present. Another had to do with the modes of inheritance between ancestors and offspring, with which the past three chapters have dealt and with which the three following chapters will be concerned. The third problem listed was that of the manner in which the characters latent in the zygote became patent in the resulting offspring.

Thus far we have talked about genes and about their final end products, characters, without attempting to say how the genes finally come to express themselves as they do, or, in other words, what the causal relation is between genes and chromosomes and expressed characters. We have pointed out that development results from the actions and interactions of genes, cytoplasm, and environment, and that, although certain genes are known by some final character, there are often many other concomitant developments, as though this gene had one major and many minor effects, and, finally, that most characters depend on the combined interactions of many genes rather than on the specific action of one individual pair of genes.

We know that the genes determine both the general characteristics of an organism, *i.e.*, to what species it will belong, as well as its individual characteristics. We know too that all the nucleated somatic cells have identical sets of complete chromosomes and genes. Although the genes might function at different rates at different times, it seems obvious that genes alone do not condition differentiation, but that we must invoke gene interactions; gene and cytoplasmic interactions; gene, cytoplasmic, and environmental interactions; as well as gene and cytoplasmic productions to explain developmental differentiation and development.

Sinnott and Dunn have pointed out that size differences are only differences in amount of growth and that these may be due to differences in size of the early embryo, to differences in rate of growth, or to differences in duration of growth, all of them under gene control. In animals,

growth depends on hormonal stimulation from the anterior pituitary, which has been shown in mice to have a genetic basis. In several plants it has been shown that there is a direct correlation between the size of a very young ovary primordium "embryonic capital" and the size of the eventual fruit, and in animals Gregory and Castle have shown that as early as 40 hours after fertilization the embryos of a large race of rabbits are significantly larger than those of a small race. The duration of growth accounts for the differences in size between dwarfs and giants of the same species, for the size of cells is approximately the same in both.

Likewise differences in shape or size of organs or parts are known to have a genetic basis, *e.g.*, comb shapes in fowl (rose, pea, walnut, single), fruit shape in squash (club, spherical, disk), length of legs in sheep (Ancon), and length of rabbit ears. Here the genes influence the amount or differentiation of growth in parts or in one direction at the expense of another. The reduced growth rates of legs and wings of creeper fowl have been shown by Landauer to be in evidence at the seventh day of incubation.

Kuhn and his associates found that color of various parts of the European flour moth was due to a dominant gene *A*, and Caspari showed that testes of the *AA* or *Aa* genotype transplanted to *aa* host not only retained their color but caused a certain amount of color to develop in the normally colorless *aa* host, and that colorless *aa* ovaries or brain transplanted to *AA* or *Aa* hosts took on color, due presumably to a hormone secreted by *A* tissues. Similarly, through transplantation procedure in Drosophila, Beadle and Ephrussi have demonstrated a chain of two hormonal substances to be necessary for the production of the wild-type red eye color. Wright has offered a theory involving oxidizing enzymes to explain the color patterns in guinea pigs. Melanin pigments are known to be formed from colorless chromogens in the cytoplasm. Wright assumes two enzymes in the nuclei of cells capable of oxidizing chromogens to varying degrees. One of these is assumed to be necessary for the production of any color, and, when present alone, produces red. The other, nonfunctional in the absence of the former and producing no effect by itself, when present in the full amount together with the first, produces black color, and in lesser amount produces brown. Genes evidently control the presence and amount or absence of these enzymes as well as their potency. Albinism is presumably due to a lack of the first enzyme, and various modifying genes affect the expression of the second enzyme. Somewhat comparable theories of color in plant have been proposed by Scott-Moncrieff, Lawrence, and Wheldale.

The work of Beadle and others[1] with the mold *Neurospora* is con-

[1] BEADLE, G. W., Biochemical Genetjcs, *Chem. Rev.*, **37**:15–96, 1945.

sidered classic in this field. A number of mutant strains have been produced as a result of X rays. It has been found that the growth of some of these mutants is limited in the absence of a specific vitamin of the B-complex. When the vitamin in question is added, normal growth occurs. Some strains require pantothinic acid, some strains require niacin, and others are limited by thiamin, riboflavin, or other members of this group. It has been concluded that the inability of the mutant strains to grow in the absence of these specific vitamins is the result of the modification of specific genes which limits or inhibits the production of a specific enzyme needed for the synthesis of the vitamin in question. Other mutants require various amino acids.

The amounts of various genes have been shown in both plants and animals to have a distinctive effect on certain characters. Since the endosperm of corn is normally triploid, races can be made up containing none, one, two, or three of the dominant *Y* genes for yellow color. Mangelsdorf and Fraps have shown that these varying amounts of the Y gene are directly correlated with the relative amount of vitamin A present, *yyy* endosperm having 0.05 rat units, *Yyy* 2.25, *YYy* 5.00, and *YYY* 7.5. Dosage data are also available in Drosophila, where the gene *sv*, shaven (bristles and hairs removed), in the IV chromosome can exist in the haplo-IV form (only one of the IV chromosomes present), as well as the normal diplo IV (two IV chromosomes), triplo, and tetra forms. In a fly with only one IV chromosome containing the recessive *sv* gene, the shaven condition exists in extreme form, less extreme in a diplo form, still less in a triplo form, and where four of the IV chromosomes are present (tetra form), each containing the recessive gene for shaven, the bristles and hairs are about normal. In other words four recessive genes do about the same job as two dominants.

In the eggs of some of the lower forms, the general pattern of development is already laid down before fertilization; *i.e.*, it is determined by the genes of the mother. In snails, right- or left-handed coiling is determined by the cytoplasm of the mother. This in turn is affected directly by the genetic constitution of the mother in which the egg was formed. Right-handed coiling is dominant, so that a cross between a homozygous right *DD* and left *dd* shows right-handed coiling *Dd*. The F^1 *DD*, *Dd*, and *dd* are all coiled to the right (because the mother did), but the last class, *dd*, give all left-handed coiling offspring.

In some instances the genes make their presence felt right from the start. In corn, for example, ordinary pollen (starchy) stains blue with iodine, whereas pollen from mutant waxy plants stains reddish-brown owing to the production of a different enzyme. When a cross is made between starchy and waxy, however, the hybrid produces two sorts of

pollen, the one with the starchy gene staining blue, the other with the waxy gene reddish-brown.

In some cases the genes delay their action for a short while. In the higher species the anlagen of both male and female genitalia are present after the first few weeks of embryonic life. Then apparently the different gene complexes come into play, and the primordia of one sex develop to maturity, whereas those of the other atrophy. There are other character-

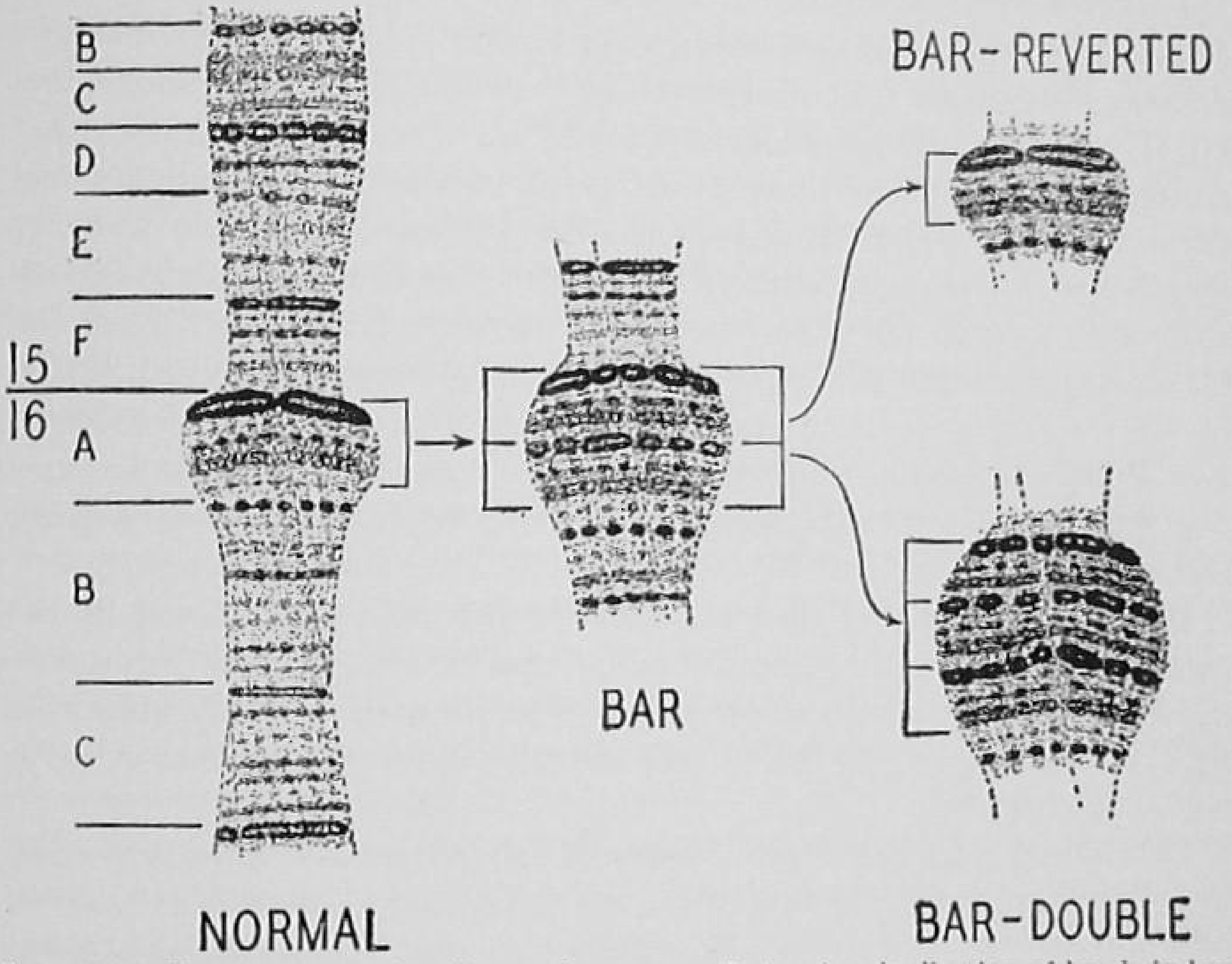

FIG. 110.—The bar region in salivary chromosome I, showing duplication of bands in bar and double-bar. (*From Bridges, after Sinnott and Dunn.*)

istics that may remain latent for a considerable time after birth, and some do not appear until middle life or later.

Sturtevant and Morgan first reported a case in which the position of a gene in a chromosome apparently affects the expression of a character. This is known as *position effect*, and an example is the bar gene in Drosophila. Bar eye in Drosophila (facets in a bar pattern rather than round) has long been known as a dominant at point 57 in the X chromosome. Zelany discovered that homozygous bars very infrequently produced a normal (1 in 1,500), and, still less frequently, a still more restricted bar, or ultra or double bar. By using bar females with two other mutant genes near bar, Sturtevant and Morgan showed that the production of normals from bar was always due to a peculiar unequal crossing over.

Bridges finally, through a study of salivary-gland chromosomes, showed normal round eyes to be due to one band in the X chromosome, bar to a duplication of this band, and double bar to this band being in triplicate.

In leaving this entrancing but difficult field of the basis of genic, cytoplasmic, environmental, enzymatic, hormonal, and organizational influences in the development and organization of new characters into a completed unique whole (epigenesis), we would remind the student that any individual begins its life as a tiny fertilized egg, but that very soon the complete body pattern emerges in a very minute form, but it is definitely organized. The month-old embryo is only a few centimeters long but is definitely organized as a miniature of the adult form. All of its parts and organs are at this time closely related in space, were even more so earlier, so that the influence of one portion or organ of the body on contiguous ones is not difficult to imagine. Spemann's classic experiment in transplanting a tiny portion from near the dorsal lip of the blastopore of an early embryonic amphibian to a totally different location in another embryo with the resulting formation of a new embryo out of tissues that would normally have produced totally different structures was the first indication of definite organizing centers in the developing embryo.

It must be admitted that but little is yet definitely known of the causes bringing about differentiation and specific organization in a developing embryo, but much research is now in progress to bridge the void between the genes in the zygote and the fully developed character in the resulting organism.

Evidence Supporting Gene Theory of Inheritance.—There are many lines of evidence lending support to the chromosomal, or gene, theory of inheritance. First and foremost is the fact that almost all organisms arise from the union of an egg from the female parent and a spermatozoon from the male parent. This is all the living material the offspring gets from its parents, though, of course, it derives its materials for growth (proteins, fats, minerals, etc.) from its mother's blood. Results of breeding experiments show that, speaking generally, both parents are jointly and equally responsible for the potentialities of their offspring. Because this is so and because the two germ cells, egg and sperm, are alike only as to their nuclei, it seems logical to conclude that the determiners of potentialities are located in the two nuclei which contain the chromosomes and which in turn are made up of genes.

Additional support for the theory is to be found in the phenomenon known as *parthenogenesis; e.g.*, an organism arising from an egg that has been stimulated to cell division artificially; *e.g.*, with a hot needle. These organisms evidence maternal characteristics only. In like manner an

egg, the nucleus of which has been removed or inactivated by X rays, may be fertilized by a sperm, and in this case the organism will evidence paternal characteristics only.

Further evidence is available from cytological studies, which have demonstrated that, if one of the small (IV) chromosomes in Drosophila is lost from an egg or sperm, the resulting offspring is different from a normal fly in many parts of the body; *i.e.*, specific effects are produced by this IV chromosome. For example, if a female with normal eyes but having only one IV chromosome is mated with a mutant eyeless male, half the offspring are eyeless, and they are also weak individuals, many of them not getting through the pupal stage successfully. This proves that the gene for the eyeless condition is located in the small IV chromosome.

The behavior in inheritance of sex-linked characters, *i.e.*, characters determined by genes located in the sex chromosomes, is additional strong evidence that the genes located in the chromosomes of the nuclei of the sex cells, ova and spermatozoa, are the actual determiners of the potentialities of any organism.

Finally the work of Stern, with Drosophila, and Creighton and McClintock, with maize, which demonstrates a complete correspondence between genetic and cytological crossing over, seems to furnish the final bit of positive proof for the complete substantiation of the chromosomal, or gene, theory of inheritance.

Summary of Modern Genetic Theory.—The modern theory of inheritance is based upon the behavior in gametogenesis and ontogeny of more or less hypothetical entities called *genes*. However, the theory has now been tested by means of thousands of planned breeding experiments and has been corroborated by numerical data, as indicated in the definite numerical ratios for the mono-, di-, tri-, and polyhybrids. In other words, the theory is no longer a theory but an established fact. It should be recalled that the facts of breeding came first and the theory to explain the facts came second. We demand two things of any theory: (1) that it logically explain events that have transpired in the past, and (2) that its principles enable us successfully to predict future happenings. These criteria of fitness have been successfully met by the chromosomal, or gene, theory of inheritance.

In brief, the gene theory assumes that the characteristics of an organism are conditioned by paired genes located at similar loci in homologous chromosomes; that one member of a gene pair may dominate the situation more or less fully in the developed organism, so that the other member of the pair is not externally recognizable; that the genes are organized into groups, each group forming a chromosome; that at the reduction division in gametogenesis one member of each homologous pair

of chromosomes is found in each daughter cell; that the distribution of the homologous chromosomes to the daughter cells is at random; that previous to reduction, *i.e.*, during synapsis, equal interchanges of chromatin material may take place between the nonsister chromatids; and that the chromosomes are always organized in a definite manner, each gene in its inviolable place and the genes arranged in a linear series.

Later chapters will indicate how the genes may change, thus giving rise to new variates. Once again the writer would like to caution against any tendency to oversimplify the matter of the genes and their behavior in inheritance. The genes themselves are probably very complex in their structure. They are very closely associated with the cytoplasm of the cells, and full development of the individual should be looked upon as a result of the interactions between the genes themselves, between the genes and the cytoplasm of the cells, and between the cells and their environment. It is the interactions and interrelations of all these forces that function in the development of a new individual rather than the individual actions of separate genes.

It is known, for instance, that in Drosophila at least 50 pairs of genes function in bringing about the development of the normal red eye. It is also known that a change at locus 44.4 in the I chromosome, a change at locus 54.5 in the II chromosome, or a change at locus 49.7 in the III chromosome will each result in purplish rather than red eyes. These genes have been named *garnet*, *purple*, and *maroon*, respectively. It would be possible, therefore, to mate two purple-eyed individuals and to get from them all normal red-eyed offspring, for each parent might supply the missing normal gene that the other lacks. It is also readily seen that one type of purplish eyes (garnet) would show sex-linked inheritance, for this gene is located in the sex chromosome, whereas the other two sorts of purplish eyes (purple and maroon) would show ordinary Mendelian inheritance.

As has been shown earlier, dominance is a relative term, and a characteristic that is dominant in one type of mating may be recessive in another. Inheritance, therefore, should be looked upon as the interaction between genes, cytoplasm, and environment rather than thought of in an absolute sense.

Summary.—In this final chapter dealing with the principles of inheritance, we have considered the complications introduced into breeding data by the fact that many genes may be located in one chromosome, so that these genes do not assort independently, although the chromosomes always do so. We have seen that varying degrees of linkage up to 100 per cent may be encountered. If linkage is not complete, various amounts of crossing over up to nearly 50 per cent may be encountered,

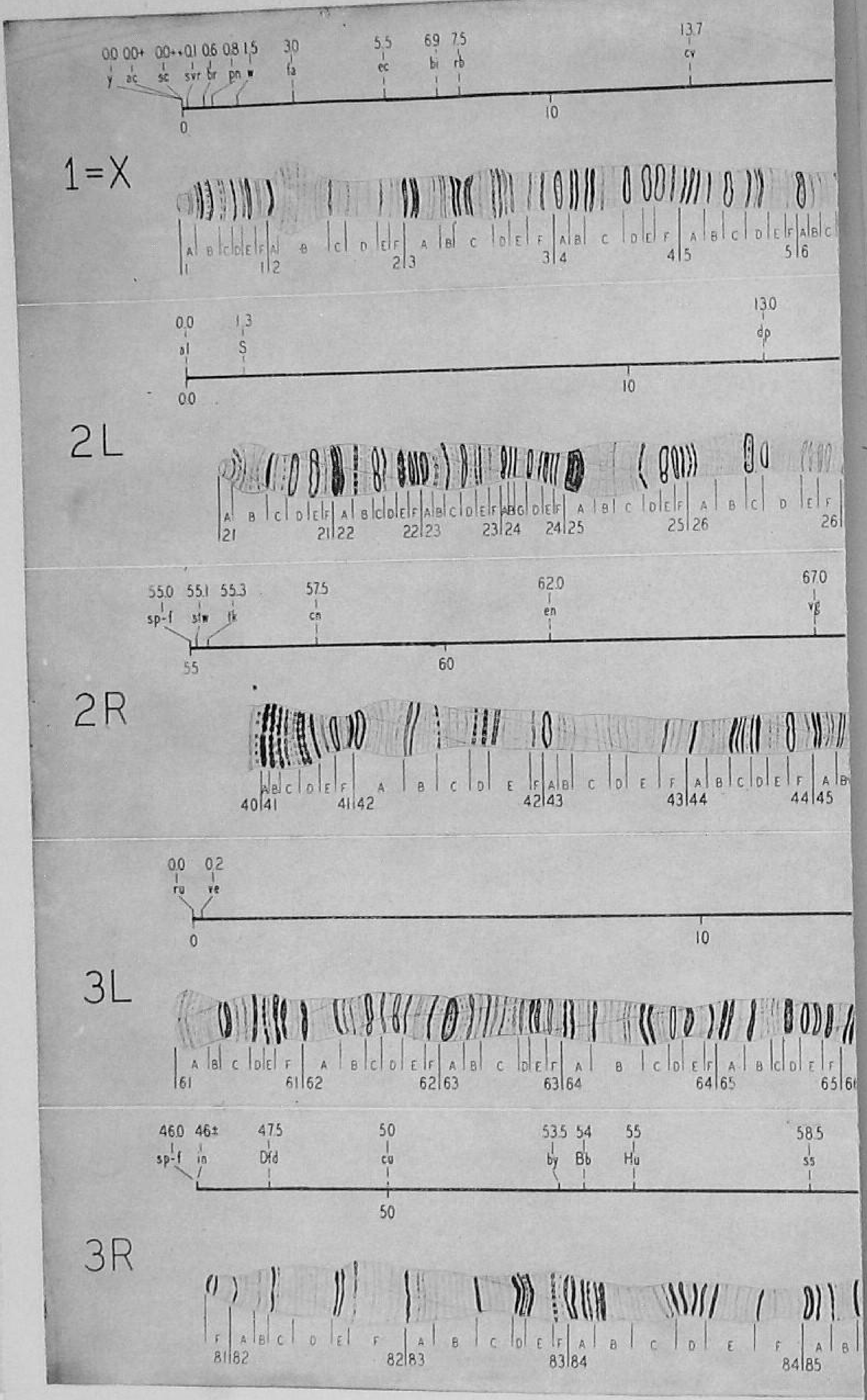

FIG. 111.—Bridges' map of the chromosomes o

...ary gland cells of *Drosophila melanogaster* (as in 1936) compared with partial genetic maps showing the locations of some of the important gene-loci. (*From Sinnott and Dunn, courtesy of C. B. Bridges and the Journal of Heredity.*)

the salivary gland cells of *Drosophila melanogaster* (as in 1936) compared with partial genetic maps showing the locations of some of the important gene-loci. (*From Sinnott and Dunn, courtesy of C. B. Bridges and the Journal of Heredity.*)

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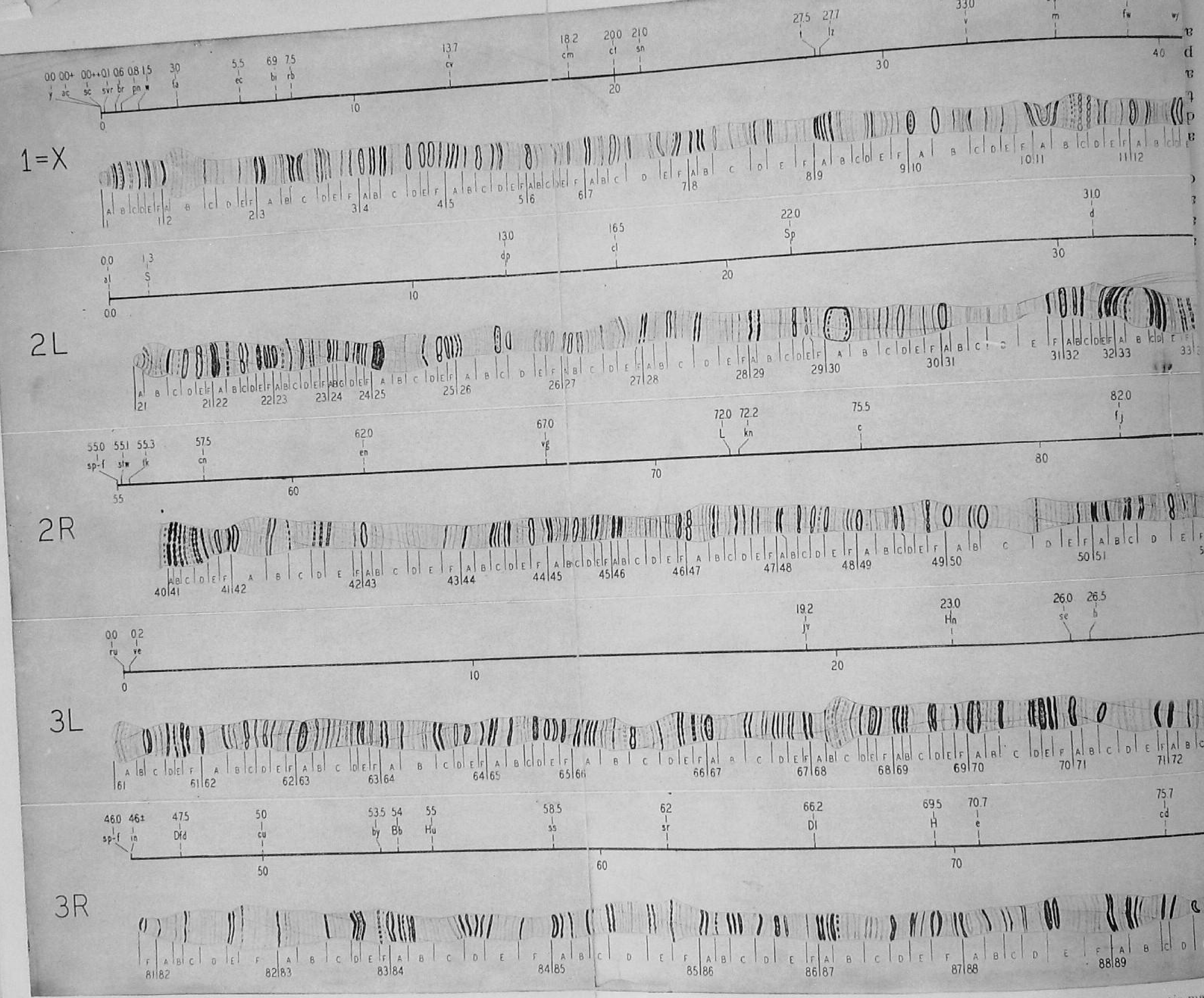
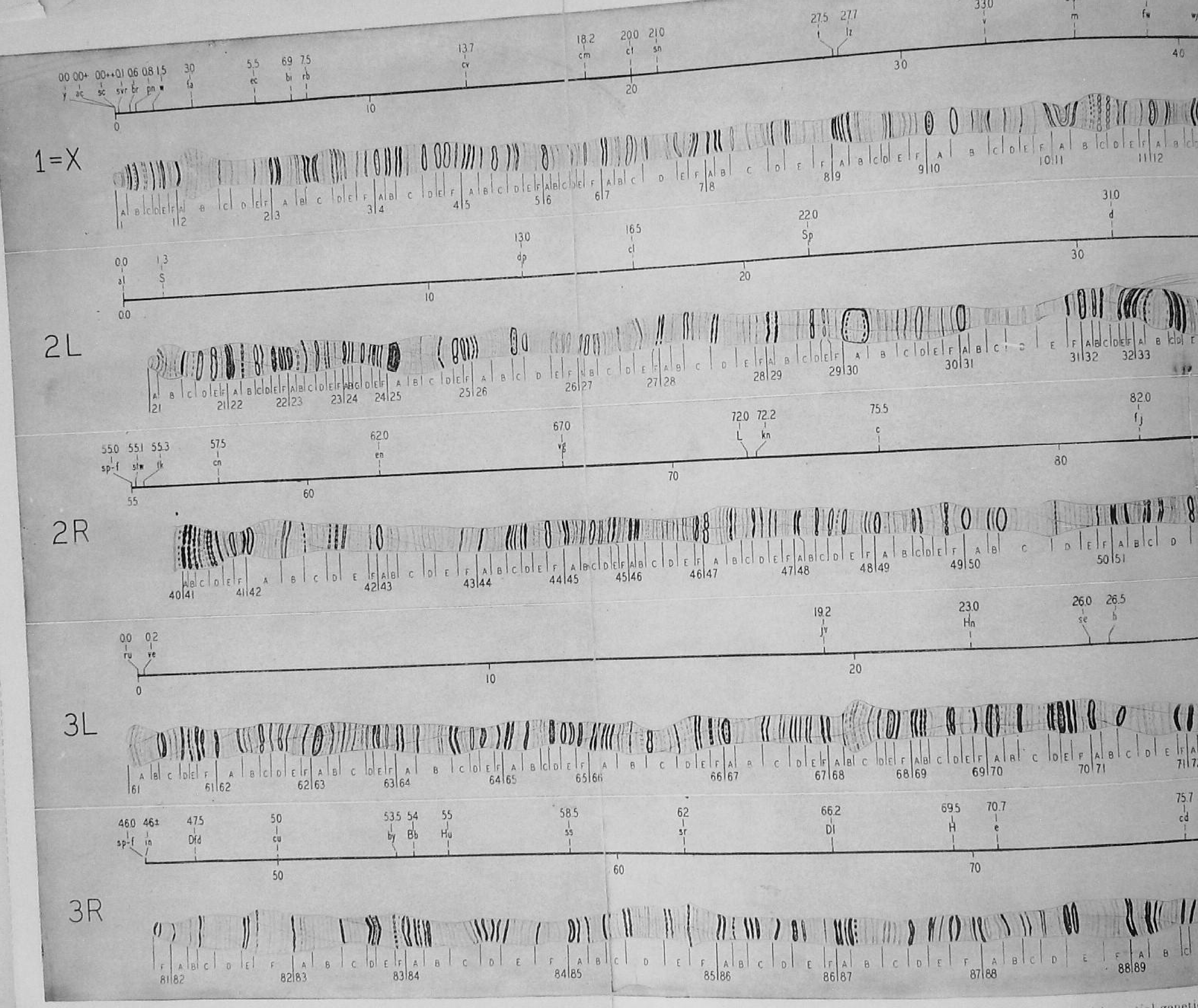


(... 1936) compared with partial genetic ma



1=X
2L
2R
3L
3R
00 y
00+ ac
00++ sc
01 svr
06 br
08 pn
15 w
30 fa
5.5 ec
69 bi
7.5 rb
13.7 cv
18.2 cm
20.0 ct
21.0 sn
27.5
27.7 lz
33.0 v
m
fw
0.0 al
1.3 S
13.0 dp
16.5 cl
22.0 Sp
31.0 d
55.0 sp-f
55.1 stw
55.3 fk
57.5 cn
62.0 en
67.0 vg
72.0 L
72.2 kn
75.5 c
82.0 fj
0.0 ru
0.2 ve
19.2 jv
23.0 Hn
26.0 se
26.5 b
46.0 sp-f
46± in
47.5 Dfd
50 cu
53.5 by
54 Bb
55 Hu
58.5 ss
62 sr
66.2 Dl
69.5 H
70.7 e
75.7 cd

and crossover values between any two genes remain constant under uniform conditions. The use of crossover values in constructing the very ingenious chromosome maps was indicated on the basis of the genes being arranged in linear series along the chromosomes. We completed our discussion of the seven Mendelian principles with references to interference and to limitation of the linkage groups to the number of pairs of chromosomes present in any species. Finally, we discussed the as yet rather incompletely known role of the genes in development, indicated the various lines of evidence that substantiate the chromosomal and gene theory of inheritance, and presented a summary of the modern genetic theory.

References[1]

Problems

1. Assume that genes *a* and *b* are linked and show 40 per cent of crossing over. If a ++/++ individual is crossed with one that is *ab*/*ab*, what will be the genotype of the F_1? What gametes will the F_1 produce and in what proportions? If the F_1 is crossed with a double recessive, *ab*/*ab*, what will be the appearance and genotypes of the offspring?

2. If the original cross is +*b*/+*b* × *a*+/*a*+, what will be the genotype of the F_1? What gametes will it produce? If the F_1 is crossed back with a double recessive, what will be the appearance of the offspring?

3. An individual homozygous for genes *cd* is crossed with wild type and the F_1 crossed back to the double recessive. The appearance of the offspring is as follows: 903 ++, 898 *cd*, 98 +*d*, 102 *c*+. Explain this result, giving the strength of the linkage between *c* and *d*. If assortment between *c* and *d* were independent, what would be the result of this cross?

4. If the cross in the preceding question had been between a homozygous +*d* individual and a homozygous *c*+ one, what would be the result of the cross between F_1 and the double recessive?

5. How far apart are *A* and *B* if in the F_2 you derive 706 *AB*; 291 *Ab*; 304 *aB*; 697 *ab*?

6. Results of a cross of *Aa Bb Cc* × *aa bb cc* give:

600 *ABC*	140 *aBC*	15 *aBc*
580 *abc*	120 *Abc*	5 *AbC*
	130 *abC*	
	120 *ABc*	

What are the percentages of crossing over between *A* and *B* and *B* and *C*? How far apart are A and *C*?

7. Note.—In Drosophila the mutant known as *black*, *b*, has a black body in contrast to the wild type, which has a gray body; and the mutant *arc*, *a*, has wings which are somewhat curved and bent downward, in contrast to the straight wings of the wild type.

In the two following crosses the parents are given (homozygous in each case) together with the counts of the offspring of F_1 females bred to black, arc males (data from Bridges and Morgan).

[1] See lists at end of Chaps. XI and XII.

a. Black, arc × wild type (gray, straight)

F_1 females × black, arc males give

1,641 gray, straight.
1,251 gray, arc.
1,180 black, straight.
1,532 black, arc.

b. Black, straight × gray, arc

F_1 females × black, arc males give

281 gray, straight.
335 gray, arc.
335 black, straight.
239 black, arc.

From these data calculate the crossover value between black and arc.

8. Note.—In Drosophila the mutant known as *vestigial, v,* has wings that are very much reduced as compared with the long wings of the wild type.

In the two following crosses the parents are given, as in the previous question, together with the counts of offspring of F_1 females crossed with black, vestigial males (data from Bridges and Morgan).

a. Black, vestigial × wild type (gray, long)

F_1 females × black, vestigial males give

822 gray, long.
130 gray, vestigial.
161 black, long.
652 black, vestigial.

b. Black, long × gray, vestigial

F_1 females × black vestigial males give

283 gray, long.
1,294 gray, vestigial.
1,418 black, long.
241 black, vestigial.

From these data calculate the linkage strength between black and vestigial.

9. Note.—In tomatoes, Jones has found that tall vine is dominant over dwarf, and spherical fruit shape over pear. Vine height and fruit shape are linked, with a crossover percentage of 20 per cent.

If a homozygous tall, pear-fruited tomato is crossed with a homozygous dwarf, spherical-fruited one, what will be the appearance of the F_1? Of the F_1 crossed with a dwarf, pear? Of the F_2?

10. A certain tall, spherical-fruited tomato plant crossed with a dwarf, pear-fruited one produces 81 tall, spherical; 79 dwarf, pear; 22 tall, pear; and 17 dwarf, spherical. Another tall, spherical plant crossed with a dwarf, pear produces 21 tall, pear; 18 dwarf, spherical; 5 tall, spherical; and 4 dwarf, pear. What are the genotypes of these two tall, spherical plants? If they were crossed, what would their offspring be?

11. NOTE.—In rats dark eyes are due to the interaction of two genes *R* and *P*, the recessive allele of either producing light eyes. These genes are in the same chromosome.

When homozygous dark-eyed rats, ++/++, were crossed with double-recessive ones, *rp*/*rp*, and the F_1 crossed back with the double recessive, the following offspring were obtained (data from Castle): 1,255 dark-eyed; 1,777 light-eyed.

When +*p*/+*p* animals were crossed with *r*+/*r*+ ones and the F_1 crossed back with the double recessive, the following offspring were obtained: 174 dark-eyed; 1,540 light-eyed.

Calculate the linkage between *r* and *p*.

12. In the fowl, assume that *e* (early feathering) and *B* (barring) are sex-linked and show 20 per cent of crossing over (in the male only). If a male from a cross of late-feathered, barred male with early, black female is mated with an early, black female, what will be the appearance of their offspring, as to feathering and barring?

13. Assume that genes *a* and *b* are linked, with a crossover percentage of 20 per cent; and that *c* and *d* are also linked, with a crossover percentage of 10 per cent, but are in another chromosome. Cross a plant homozygous for *ABCD* with one which is *abcd* and cross the F_1 back on *abcd*. What will be the appearance of the offspring of this cross?

14. In Drosophila, yellow body is sex-linked and recessive to the gray body of the wild fly. Vermilion eye is also sex-linked and recessive to the wild red eye. The genes for yellow and vermilion show about 28 per cent of crossing over. The gene for vestigial is in one of the autosomes. If a homozygous yellow-bodied red-eyed long-winged female is crossed with a homozygous gray-bodied vermillion-eyed vestigial-winged male, and if an F_1 female is crossed with a yellow, vermilion, vestigial male, what will be the appearance of the offspring of this last cross?

CHAPTER XV

THE PRINCIPLES OF VARIATION

Genetics, as was said earlier, is concerned with heredity and variation. Its task is to explain why an organism does or does not resemble its ancestors. The three previous chapters have dealt with hereditary likenesses between related organisms. Heredity is the great conserving force. The fact that the genes and their combinations are relatively stable has acted as a ratchet mechanism to hold whatever gains have been made from the standpoint of evolution. For progress, however, we need something more than this, *viz.*, variation. For many centuries, species and varieties were believed to be immutable. The rise of many varieties of dogs from one or two remote ancestors by means of the principles of variation and selection and the same phenomenon in horses, cattle, sheep, and swine was pointed out in an earlier chapter.

Henry van Dyke is reported to have said that there is one thing in which all men are exactly alike, and that is that they are all different. This statement also holds true for farm animals. To the observing it is quite evident that "the most invariable thing in nature is variation."

When we consider that probably no two blades of grass, no two calves, and no two human beings have ever been just exactly alike (though identical twins are essentially so), we get a fleeting glimpse of the resourcefulness of nature. It would seem that the new plans and specifications must sometime be depleted, yet life flows along in its thousands of varieties and millions of unique individuals, each different from all the rest of its kind. Fortunate, too, that this is so, because without this principle progress would be impossible. As has been said, "Variation is at once the hope and the despair of the breeder," the hope because through it may be produced offspring better than their parents, the despair because after animals have been greatly improved, they may and very often do vary again toward mediocrity.

That animals vary in size, type, rate of growth, efficiency of feed conversion, quality of carcass, proportion and distribution of fat and lean, wool quality and quantity, fertility, longevity, resistance to disease, milk production, butterfat percentage, color of milk, persistency, speed, stamina, style, tractability, color, and in a hundred other ways is too evident to need much discussion.

Here are two steers, one of them gains 22.1 lb. for each 100 lb. of nutrients fed; the other only gains 14.3 lb. from a like amount of feed.

Here are the litters of two sows, one of them gains 100 lb. from 504 lb. of feed; the other litter gains 100 lb. from 360 lb. of feed.

Here are two dairy cows, one of them returns 36 lb. of total digestible nutrients for each 100 lb. fed; the other returns only 18 lb. from a like amount of feed.

Here is a Guernsey bull bred to 8 cows that range from 12,500 to 13,500 lb. of milk per year; the 8 daughters range from 8,600 to 15,600 lb.

Here is an Ayrshire bull bred to 13 cows that range from 10,500 to 11,500 lb. of milk per year; the 13 daughters range from 7,800 to 15,300 lb.

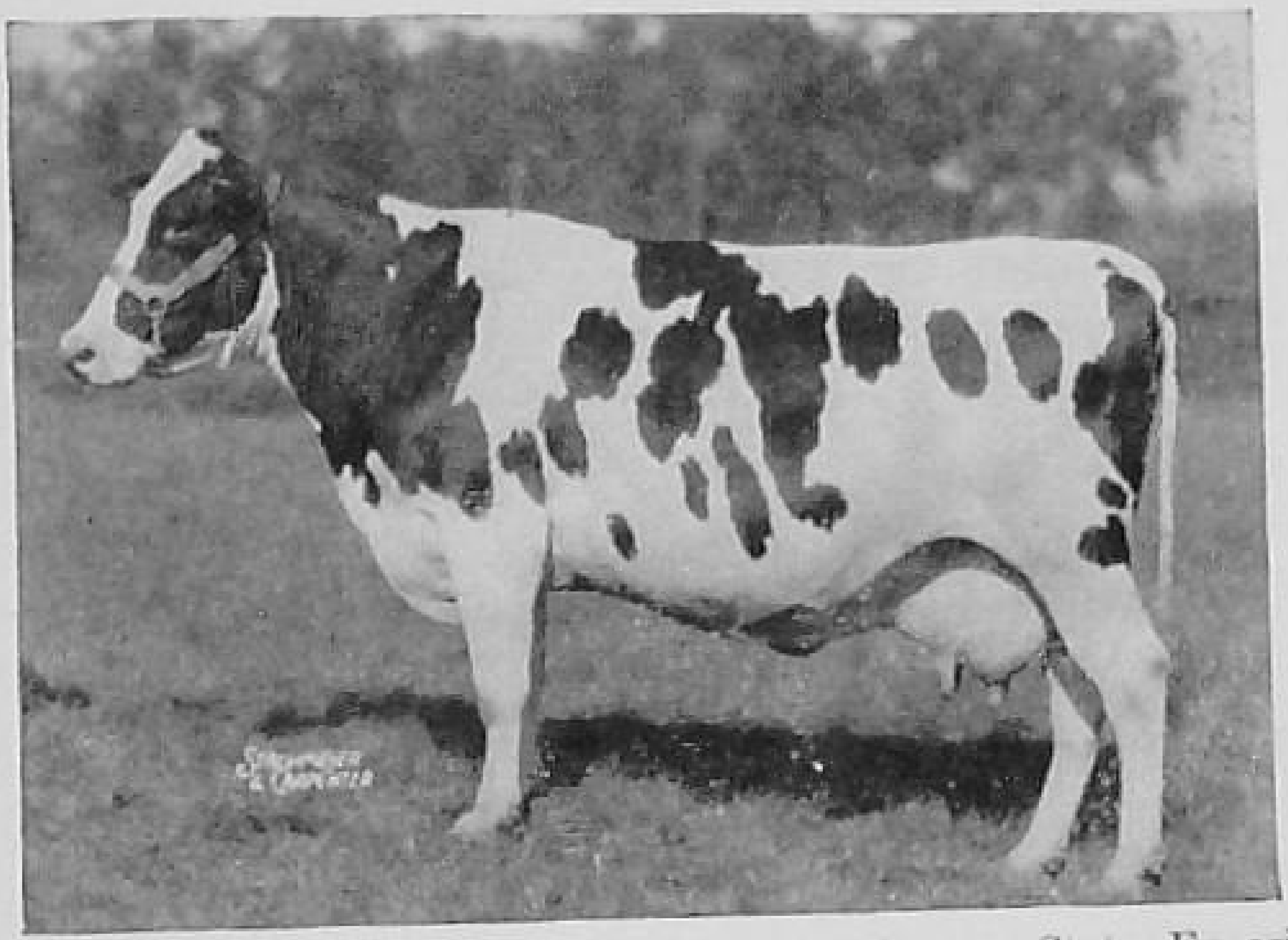


FIG. 112.—Beth of Amherst 3rd, a Grand Champion at Eastern States Exposition (picture taken when dry). Her twin sister was nearly as poor a dairy type as this one is good.

Variation is tremendous, partly owing to the mechanism of inheritance, partly to the effects of environment. Most of the qualities of our animals are elastic. Depending on feed, care, etc., a cow may produce 8,000 lb. of milk in a year or 16,000 lb. A sow may farrow ten 3-lb. pigs and raise them all, or seven 2-lb. pigs and raise four of them. The breeder's task is to provide the best possible environment at all times and to make the environment as uniform as possible in order that his variations will be known to have a genetic basis.

Causes and Types of Variation.—There can conceivably be but two causes of genetic variation. It is caused either by some outside, supernatural force, or else it is inherent in the nature of living things, their natural response to stimuli.

Variations { Supernatural
Natural

General opinion leans toward the latter explanation. There are two types of stimuli that might conceivably bring about variation, one internal, the other external to the organism. Any fully developed organism is the result of the combined action of these internal and external stimuli.

Variations	Autogenetic
	Exogenetic

The organism starts as a single-celled zygote, with its full complement of genes derived from both paternal and maternal sources. This genetic heritage has a tendency to develop in a certain definite way, owing to its chemical and physical make-up. The norm for this new individual may vary from that of one or both of its parents because of its different chromosomal content. During intrauterine development, any organism is subject to various influences from its mother, with whom it lives in very close association. Chemical products in the blood of the mother may be transfused into the circulation of the embryo and may react in various ways on the developing embryo or cause it to react in a variety of ways. The mother's blood, or the fluid surrounding each cell, may contain nutritive material that will assist in the proper growth and full development of the embryo. On the other hand, they may contain waste or toxic products, secretions or hormones from various glands, etc., any of which may cause the embryo to vary more or less from its original normal tendencies. Effects due to the parent's habits or to contingencies in the developing embryo itself cause many variations to appear in the fully developing organism, all the way from a doubling of parts, through various types of changes, including blemishes and malformations to an entire pinching off or absence of the part.

Variations	Germinal	Recombinations
		Gene and chromosome mutations
	Somatic	Changes in soma, behavior, etc.

In this chapter, we shall consider only those variations that have their origin in the germinal material, the genes and chromosomes in the germ cells, leaving the somatic variations to be treated in the next chapter.

Variation as a Tool.—Variation is one of the most useful tools that the breeder possesses. It provides him the raw material from which he can fashion better animals. The breeder is constantly on the lookout for desirable types of variation. He sees variation as it manifests itself in his animals and seizes upon it in the hope that it will prove to be hereditary. Much variation does have a genetic basis, much of it too is environmental, whereas some perhaps is both. It is no simple

matter to separate these three categories. In addition to these complications is the further one that the hereditary variations may be of various sorts. Some of the allelic pairs of genes may show varying degrees of dominance, from complete to an entire lack. This same feature of dominance between different pairs of genes known as *epistasis* may be operating, whereas in still other cases the various genes may behave in a cumulative or additive fashion. To secure desirable variation of a hereditary sort and to guide it toward some preconceived ideal of perfection is the problem that the breeder constantly struggles with.

Fortunately there is generally plenty of variability available. In horses, cattle, sheep, and swine there are literally all sorts. The animals

Fig. 113.—Graph of Holstein Indexes, Vol. 11, *Holstein-Friesian Red Book.*

of a breed, as far as their commercially valuable qualities are concerned, probably simulate a normal curve. Some of them are poor, a few more mediocre, most of them just average, a few very good, and a very few excellent, the excellence probably being due in most cases to good heredity plus good environment. This general feature of variability is shown in Fig. 113, a graph of 703 Holstein bulls listed with their indexes.[1]

The above graph shows that 5 of these bulls had indexes of 6,000 lb. of 3.5 per cent milk, 7 had indexes of 7,000 lb. of 3.5 per cent milk, 11 indexes of 8,000 lb., etc., up to 4 bulls with indexes of 22,000 lb. and 4 with indexes of 23,000 lb. of 3.5 per cent milk. Because the index is computed from a comparison of dams' and daughters' records, it is obvious that the females would also show this sort of normal curve of production. The breeder is, of course, trying to make his selections from animals in the upper half or top quarter of these curves, and he

[1] From Vol. 11 of the *Holstein-Friesian Red Book.*

hopes that a goodly part of this variation is hereditary and will be passed along to the offspring.

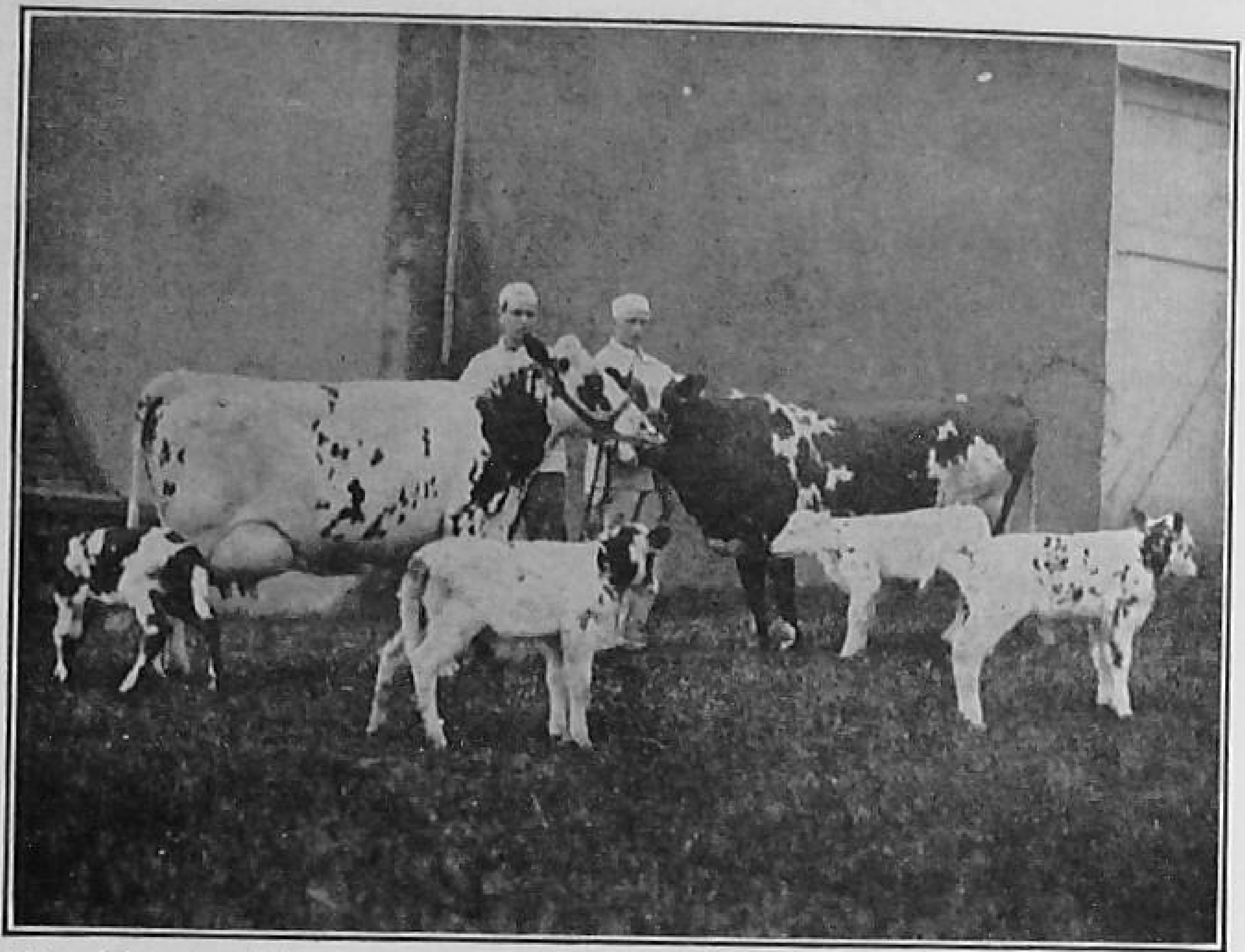


FIG. 114.—Two Ayrshire cows and their twin calves showing marked variation in amount of red color in the coat.

Freeman[1] found the mean number of body vertebrae of 52 Duroc pigs to be 20.52 ± 0.067, and for 79 Yorkshire pigs to be 21.27 ± 0.046. The increased number of vertebrae were associated with greater body length, which would add to carcass value and might possibly be correlated with greater fertility.

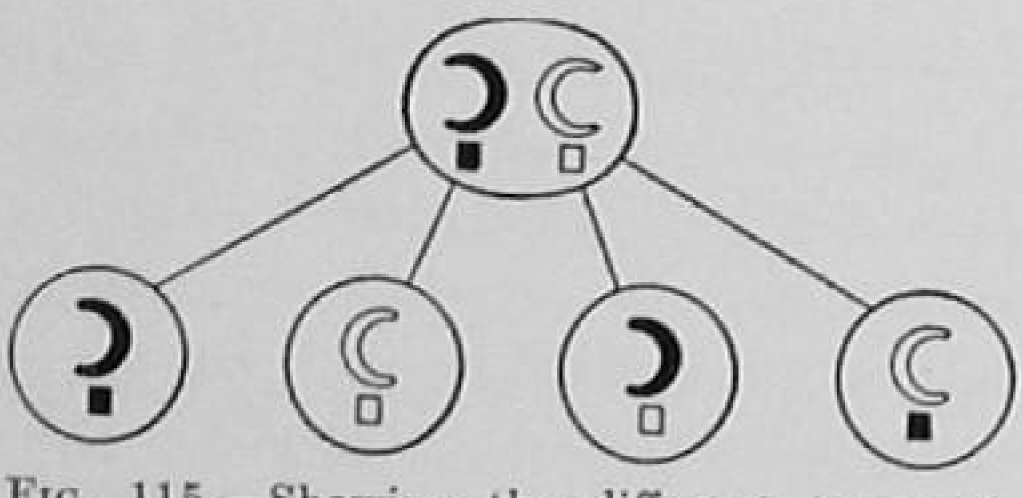


FIG. 115.—Showing the different types of germ cells possible in a species with two pairs of chromosomes—chromosomes remaining intact.

Variations from Recombinations.—We have already discussed pretty thoroughly the general proposition of recombinations of chromosomes during meiosis. In an organism with two pairs of chromosomes, there are four possible ways of recombining these intact chromosomes as indicated in Fig. 115.

In each resulting germ cell there must necessarily be one member of each pair of chromosomes. The possible numbers of different gametes

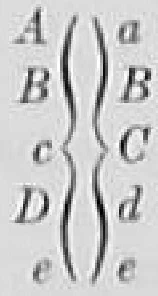
[1] FREEMAN, V. A., Variations in the Number of Vertebrae in Swine, *Jour. Hered.*, **30**(2):61–64, February, 1939.

with some varying numbers of pairs of chromosomes are shown in Table 23.

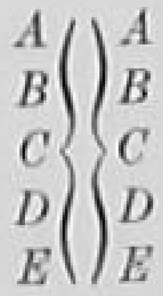
TABLE 23.—NUMBER OF DIFFERENT KINDS OF GERM CELLS POSSIBLE FROM VARYING NUMBERS OF PAIRS OF CHROMOSOMES

	Number of pairs of chromosomes	Number of different kinds of germ cells	
Ascaris	1	2^{1}	2
A. megalocephala	2	2^{2}	4
Drosophila melanogaster	4	2^{4}	16
Corn	10	2^{10}	1,024
Swine	19	2^{19}	524,288
Human	24	2^{24}	16,777,216
Cattle, goat, horse	30	2^{30}	1,073,741,824

It is evident from the above table that the simple recombination of intact chromosomes in the higher species can account for a tremendous amount of variation. From a perusal of the above table one might conclude that breeding is a pretty haphazard and impossible task anyway. The writer would not try to maintain that it is easy, but neither is the job as impossible as might appear at first glance. What we are trying to do from a practical breeding standpoint is to make our animals pure for genes that lead to the development of desirable characters. At present they are rather heterozygous and therefore do not breed true. Two homologous chromosomes may bear the following sorts of genes.



If, by selecting, we bring it about that these two chromosomes become homozygous,



then it will make no difference which one of these two homologous chromosomes go to any egg or sperm, for they are now exactly similar. It would still and always be true that the 30 pairs of chromosomes in cattle could and would be capable of producing over a billion different

recombinations, but, if our animals were entirely homozygous, all of these billion combinations would be identical. It seems unlikely that we can ever reach this goal, but the fact remains that the more heterozygosity can be reduced, the less variation we will have.

If a male *Aa* is mated to a female *Aa*, there can be produced two different types of gametes (*A* or *a*) by each parent and offspring of three different genotypes (*AA*, *Aa*, or *aa*).

If a male of the genetic constitution *Aa Bb* (with genes *A* and *B* in different chromosomes) is mated to a female of the same genetic make-up, there can be produced four different types of gametes by each parent and offspring of nine different genotypes.

With three pairs of heterozygous nonlinked genes in each parent, we would have eight different types of gametes and offspring of 27 different genotypes.

TABLE 24.—INDEPENDENTLY SEGREGATING GENE RECOMBINATIONS

Number of pairs of heterozygous genes	Number of different gametes	Number of different genotypes
1	2	3
2	4	9
3	8	27
n	2^n or $(10^{0.301n})$	3^n or $(10^{0.477n})$

If two animals were of the genetic constitution shown below (genes in different chromosomes),

sire, *Aa bb CC Dd*
dam, *Aa Bb cc DD*

then there would be the following possible genotypes of offspring

$$3 \times 2 \times 1 \times 2 = 12$$

Thus we could have 12 different sorts of full brothers or sisters, as to genotype, from mating the above two parents. All of these animals would have identical pedigrees but their genotypes might all be different ranging from

AA Bb Cc DD to *aa bb Cc Dd*

If the capital letters represented desirable traits and the small letters undesirable ones, we can see that there would be a vast difference between these full sisters or brothers. Identity of pedigree, then, does not mean identity of inheritance except when the parents are homozygous for each pair of genes.

Our example has dealt with four pairs of genes, or eight in all. We do not know how many genes are present in the chromosomes of our farm animals. There are 60 chromosomes in some of these animals, and, if there were an average of 100 genes in each chromosome, there would be a total of 6,000 genes. Each parent would then be transmitting not 4 genes, as in our simple example, but 3,000. If two animals were heterozygous for all of these 3,000 pairs of genes, then there could be $3^{3,000}$ different genotypes, assuming that all combinations were possible by means of independent assortment and crossing over. Such a number is, of course, beyond human comprehension. It could be written $10^{3,000 \times .477}$ or $10^{1,431}$, and it has been estimated by physicists that the whole universe contains 10^{80} electrons. Three to the nineteenth power is a number twice as large as the number of cattle at present in the world. These 3,000 genes are in bundles (chromosomes) of perhaps 100 each and, of course, will show linkage in each bundle. Even if linkage is complete in all chromosomes, we could still get 2^{30} or 1,073,741,824 different recombinations of complete chromosomes, whereas there are only about 650 million cattle in the world.

In our simple example where we were dealing with only eight genes, if we assume all these genes to be in the same chromosome the sire might be

$$\begin{matrix} A \\ b \\ C \\ D \end{matrix}\Bigg\}\Bigg\{\begin{matrix} a \\ b \\ C \\ d \end{matrix} \qquad \text{and the dam} \qquad \begin{matrix} A \\ B \\ c \\ D \end{matrix}\Bigg\}\Bigg\{\begin{matrix} a \\ b \\ c \\ D \end{matrix}$$

which would give *AbCD/ABcD*, *AbCD/abcD*, *abCd/ABcD*, *abCd/abcD* combinations.

Thus the very mechanism of inheritance in unisexual animals whereby a parent gives a sample half of his or her inheritance to each offspring is a very potent source of variation.

Variation from Crossing Over.—We learned in the previous chapter that blocks of genes in two homologous but nonsister chromatids may change places with each other. The working of this principle increases the possibility of variation to an infinite amount, so that the billion possible recombinations of intact chromosomes in farm animals fades into insignificance in comparison. Again, however, it will not be so bad as it seems if we lay our plans to render the genetic material of our animals somewhat more homozygous that it is at present.

These principles of independent assortment and crossing over make the possibilities of variations truly infinite. The workings of these principles are, no doubt, the greatest cause of variation in farm animals. They explain why a cow (scrub in this case) can be bred to a certain bull

and a heifer produced that yields 3,600 lb. of milk and later the same cow be bred to the same bull and a heifer produced that yields 6,100 lb. of milk. The first heifer yielded 31 per cent less milk than her dam, the second one yielded 17 per cent more than her dam. Or, to cite a case from the purebreds, *viz.*, a purebred cow bred twice to the same purebred bull, in the first case a heifer resulted that yielded 6,200 lb. of milk, 14 per cent less than her dam, and in the second case a heifer resulted that produced 9,800 lb. of milk, or 35 per cent more than the dam. As explained above, the chromosomes, which carry the determiners for all characters, *e.g.*, milk yield, tendency to fatten, color, speed, type, etc., go through the process of reduction, the chromosomes separating or segregating, which enables them to reunite into new combinations of various sorts. The chromosome mechanism, in heterozygous organisms, is one of the most potent causes of variation, including as it does both the recombination of intact chromosomes and the creation of different ones by means of crossing over. It must be recognized, however, that such characters as milk production may be greatly influenced by environmental factors. The occurence of such metabolic disturbances as ketosis, the presence of inflammation of the mammary gland, improper feeding, or general management practices frequently overshadow the actual genetic potentialities of dairy cattle.

Variation from Gene Mutations.—In addition to the different recombinations that might be inherited, there are mutations that are also inherited. Gene mutations are germinal or genetic variations involving single genes. They are probably due to chemical or spatial alterations in the genes for certain characteristics in the germ cells. The chemical rearrangement of the atoms in the genes that may bring about mutations might be compared to the interchanging of a certain number of hydroxyl and hydrogen ions from one place to another in the structural formula for dextrose which converts dextrose into levulose. Or different atoms may be substituted for some already present, just as one may by substitution change methane (CH_4) to monochloromethane (CH_3Cl). Both the new arrangement of atoms and the substitution of one or more different atoms for others already present would supposedly give rise to variations.

Since 1927, when Muller first discovered that treating Drosophila with varying dosages of X rays led to increased rates of mutation, much experimental work of this nature has been performed both with X rays and with radium. The evidence seems irrefutable that the bombardment of the genes by active rays does induce changes in the molecular structure of the gene, which in turn is evidenced by changes in external or physiological characteristics. These gene changes occur naturally

but at very infrequent intervals. The rate of mutational changes has been speeded up as much as 150 times by ray treatments. Some genes have proved to be much more stable than others. Stadler studied the effects of X and radium rays on seven genes in maize and found a very wide range of susceptibility to change among them. Stadler's results are shown in Table 25.

Attempts to produce mutations by chemical means go back to the early days of modern genetical research. Although some earlier work was suggestive, the first positive results indicating the production of mutations by chemicals were obtained by Auerbach[1] and Robson during the Second World War (see Auerbach, 1949, for review) with mustard gas. Since then various other chemicals have been shown to have definite mutagenic effects. A new tool is thus available to the research worker.

TABLE 25.—STADLER'S DATA ON THE FREQUENCY OF CHANGES IN SEVEN GENES OF MAIZE[1]

Gene	Gametes tested	Number of mutations	Average per one million gametes
R	554,786	273	492
I	265,391	28	106
Pr	647,102	7	11
Su	1,678,736	4	2.4
Y	1,745,280	4	2.2
Sh	2,469,285	3	1.2
Wx	1,503,744	0	0

[1] STADLER, *Jour. Hered.*, **24**, (10):372, 1933.

We do not know exactly what causes gene mutations in nature. We do know that they occur with greater or lesser degrees of frequency. About 600 gene mutations have been recorded in *Drosophila melanogaster*. One of the earliest discovered was that which changes the eye color from red to white. A white-eyed male fly suddenly appeared, and, when mated with a normal red-eyed female fly, the F_1 offspring were all red-eyed. In the F_2, however, the white-eyed condition again appeared, but only in male flies. This is, therefore, a sex-linked, recessive mutation. Other changes in this same gene have resulted in a series of 14 allelic characteristics as to eye color in Drosophila, ranging from white through ecru, tinged, buff, ivory, eosin, apricot, cherry, blood, coral, and wine to red. Reverse mutations also occur; *i.e.*, red eyes may mutate to white, and white may mutate back to red.

[1] AUERBACH, CHARLOTTE, Chemical Mutagenesis, *Biol. Rev.*, **24**:355–391, 1949.

Some gene mutations, such as lobe 2 in Drosophila, are dominants in inheritance. A great many of the mutations are lethal, the offspring never reaching maturity, whereas in others, *e.g.*, the white-eyed mutant, many other characteristics besides eye color are affected, the white-eyed individuals being less robust, more sluggish, and shorter lived.

The best known mutation among farm animals is, no doubt, the characteristic of polledness, or hornlessness. This mutation probably arose because of a chemical change of some sort in the chromosomes.

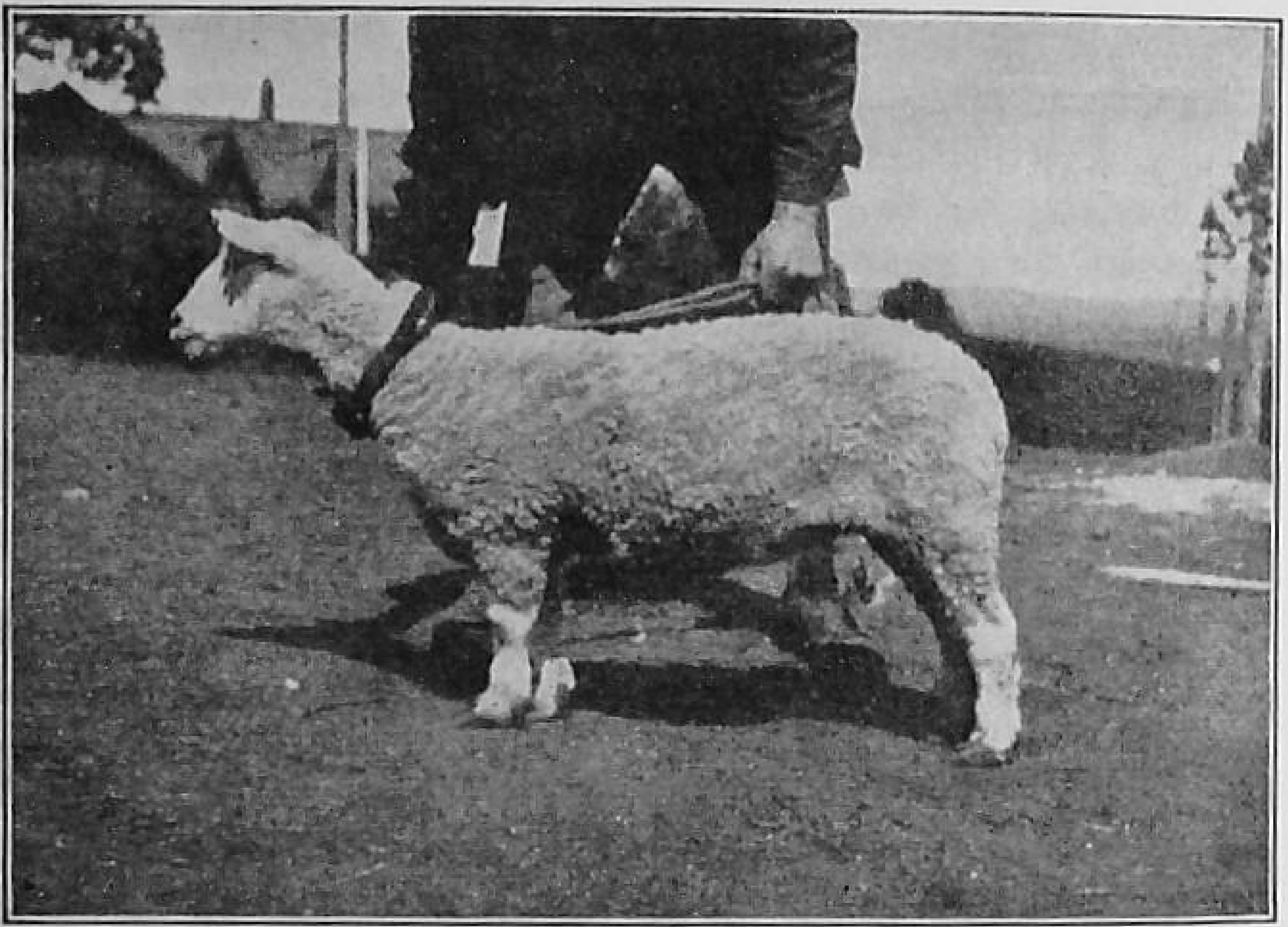


Fig. 116.—A sheep with very short and crooked legs after the style of the Ancon.

No doubt, they have arisen in all the breeds at times, and in most breeds they have been noticed and valued and a polled strain developed from them. The reason for the change in the chromosomes that prevents the horns from developing is unknown.

Another mutation, now extinct, occurred many years ago in sheep. Seth Wright, a Massachusetts farmer, had dropped in his flock a ram lamb that was a mutant, being low-backed, long-bodied, and having short crooked legs, something after the fashion of a dachshund. Farmer Wright recognized its value—its type of build, although not interfering seriously with wool production, being a decided deterrent to the sheepish pastime of fence jumping. The ram, a mutant, was used for breeding, and from this start the Ancon breed of sheep, with the characteristics listed above, was produced, though the breed has long since been supplanted by the Merino.

The Mauchamp sheep of France, with a superior sort of fleece, are sometimes considered a mutant race, but, inasmuch as the original ram was a hybrid between a Mauchamp ewe and a Dishley ram, this case, as Nathusius points out, must be removed from the records of actual mutations in domestic animals. Another character in sheep reported from Norway, *viz.*, short ears, though of no practical importance, is perhaps, a mutant.

Regarding mutations in domestic animals Babcock and Clausen state that:

> Any system of herd improvement founded on the search for and utilization of mutants is doomed from the beginning to failure, for mutants of a beneficial character appear so rarely as to have almost no practical significance. If by some fortunate chance a breeder should find himself in possession of a favorable mutant individual, however, it is a simple problem in Mendelism to establish its characters in a constant race.

For instance, if a mutant sheep were produced with no tail, a tailless breed could soon be developed and the trouble of docking saved.[1] No system of breeding has yet been advocated to produce mutations, perhaps none will ever be devised. Tendency to mutate, however, is very likely an inheritable characteristic, just as are all other features and traits exhibited by organisms.

GENERAL STATEMENTS ABOUT GENES AND MUTATIONS

1. Genes are ultramicroscopic, chemical entities—possibly giant molecules—which are fairly stable and self-propagating.
2. Gene mutations are sudden variations resulting from chemical, structural, position, or volume change in genes. If they occur in the germ cells or their primordia, they become a part of the hereditary material; if they occur in the soma, they may affect only one cell or whole groups of cells, but these somatic mutations do not become part of the hereditary material.
3. Mutation generally occurs in one gene at a time.
4. Mutation rates differ in different genes, vary from very low frequency in some genes to relatively great frequency in others, and the rates may be inherent and/or may be influenced by the environment.
5. Mutations are more likely to occur in some parts of the chromosomes than in others.
6. Mutations may involve a series of changes in one gene (multiple alleles).
7. Mutation—wild type to new allele is called *direct*.
8. Mutation—mutant allele back to wild type is called *reverse*.

[1] See *S. Dak. Agr. Expt. Sta. Cir.* 28, 1940.

9. Mutations have varying effects from almost no effect on up to a lethal effect.

10. Mutations are usually recessive and generally harmful or lethal.

11. Mutations may occur at any time—probably most frequently at maturation.

12. Mutations that are dominant show up at once.

13. Mutations that are sex-linked recessives show up at once in males.

14. Mutations occur with appreciable frequency in nature.

15. Mutations can be induced by radiation, temperature changes, and chemical agents and are proportional to the severity, within viable limits, of the treatment received.

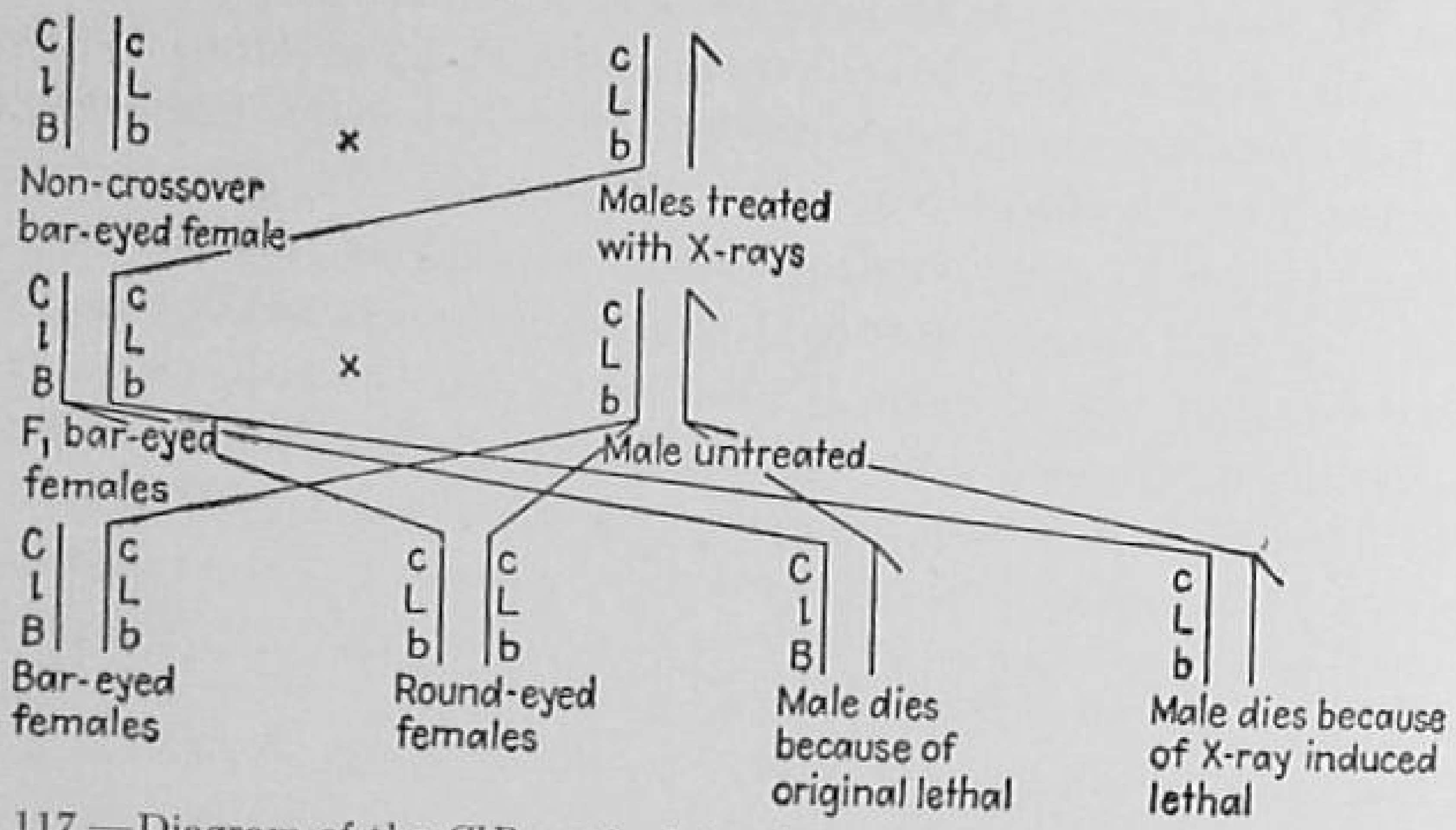


FIG. 117.—Diagram of the *ClB* method for detecting induced lethals in Drosophila.

16. Mutations must be proved by breeding experiments and analyses —white eye, probably a chemical or structural change; bar eye, gene duplication; notch, a deficiency; double bar, a position effect.

17. Several hundred gene mutations have been found in Drosophila, corn, peas (Mendel dealt with seven of them), rats, rabbits, and some, too, in the higher animals including man. Most of the problems at the end of Chaps. XII, XIII, and XIV involved gene mutations.

Lethals are generally gene mutations, and they have proved very useful in the study of mutations induced by X and radium rays. The *ClB* method was devised by Muller to study the rate of production of mutations by artificial means. Because most mutations are lethal, it was necessary to formulate a plan that would reveal their presence even though the organism was killed before hatching. To do this Muller bred Drosophila, which had the genes for crossover suppression, a known recessive lethal, and bar eyes in one X chromosome and their alleles (nonsuppressor, normal, and round eyes) in the other X chromosome

(*ClB* and *cLb*). These flies were bred to a male with nonsuppressor, normal, and round-eye genes in its X chromosome (*cLb*). Before breeding, these males were subjected to X rays. From this cross, bar-eyed females (*ClB* and *cLb*) were selected and bred to normal, untreated (*cLb*) males. From this cross, half the males will die because their X chromosomes contain the original lethal gene (*ClB*). If the other males also die (*cLb*), it shows that a new lethal mutation was produced by the X-ray treatment of the original male. The complete lack of grandsons, therefore, proves the artificial induction of a new lethal gene, probably a chemical change in some gene that destroys the balance necessary for the survival of any organism getting it.

Balanced lethals were first discovered by Muller. His stock of beaded (deformed wings) flies when mated usually gave ⅔ beaded and ⅓ normal offspring, as though beaded were due to a single dominant gene, lethal when homozygous. Muller was able to select out a stock that bred practically true for beaded (producing an occasional normal) but when crossed back to normal gave 50 per cent beaded and 50 per cent normal, showing it to be heterozygous for beaded. Full analysis by Muller finally showed that the two stocks of flies differed genetically, the first having a dominant mutation, beaded, in the III chromosome which was lethal when homozygous, the second or true-breeding strain have another lethal closely linked to beaded, so that their genetic constitution is $Bd+/+l$. With a crossover suppressor (probably an inversion) they produce only $Bd+$ or $+l$ gametes and only $Bd+/+l$ offspring (with an occasional $++$ normal if crossing over occurs), because the $Bd+/Bd+$ offspring and the $+l/+l$ offspring both die, which gives an apparently true-breeding strain because of a system of balanced lethals.

Variation from Chromosomal Aberrations.—In addition to gene or point mutations a considerable variety of chromosomal aberrations involving various-sized blocks of genes, whole chromosomes, or whole sets of chromosomes have been discovered in recent years. Changes of this nature are generally brought to light by discrepancies in breeding behavior resulting in disturbances of the normally expected Mendelian ratios, in the creation of new linkage relations, or in the appearance of variable offspring. When such things occur, cytological study has generally revealed certain changes in the number or arrangement of the loci within the whole chromosome complex or a change in the actual number of chromosomes. This close correspondence between the visible changes in the chromatin and changes in ratios or in individuals is, of course the strongest possible evidence supporting the chromosomal theory of inheritance. Since visible changes in the chromosomes result

in recognizable variations in the fully developed organisms, it seems more than justifiable to assume that the chromosomes and genes are the actual determiners of potentialities.

CHANGES IN BLOCKS OF GENES

Translocation.—It sometimes happens that a chromosome becomes broken and one of the pieces attached to some other chromosome. Bridges discovered that a group of genes that normally belonged in the II chromosome suddenly showed linkage relations with genes in the III chromosome, and this was termed *translocation*. If the piece becomes attached to a nonhomologous chromosome, a new linkage relation is set up. If, for instance, a small piece of the X chromosome in Drosophila became attached to one of the two large pairs or to the small IV chromosome, then the genes that were contained in the broken piece of X chromosome and that had formerly shown sex-linked inheritance would no longer do so. Likewise, if a piece of one of the autosomes was broken off and became attached to an X chromosome, these autosomal genes that had formerly shown ordinary Mendelian inheritance would now show sex-linked inheritance.

Such a case involving a block of autosomal genes in the II chromosome was discovered by Altenburg. This block of genes suddenly began to exhibit sex-linked inheritance as if it had become attached to an X chromosome. Cytological examination revealed the fact that one of the members of the II pair of large autosomal chromosomes was very much reduced in size, whereas one of the X chromosomes had been increased in size by just about that amount. Many cases of translocation have been studied in recent years. They are generally first evidenced by peculiar genetic behavior and then checked cytologically, though the reverse of this process has been true in a few cases.

Reciprocal Translocations.—We learned earlier that during meiosis there might be an equal interchange of various-sized blocks of genes between nonsister, homologous chromatids. This process was called *crossing over*. So too, may there be interchanges of blocks of genes between two nonsister, nonhomologous chromatids or perhaps between nonhomologous chromosomes (illegitimate crossing over). This is called *recriprocal translocation*, or *segmental interchange*. In ordinary translocation there is no trading between the chromosomes or chromatids, a section of one chromosome simply going over to another chromosome without any reciprocity on the part of the latter. In reciprocal translocation, there is reciprocity, and it is between nonhomologous chromatids or chromosomes. This type of translocation happens more frequently than does simple translocation.

If there were reciprocal translocation between one end of the II and III chromosomes in Drosophila, then at synapsis, when like genes apparently attract each other to form the synaptic knot, a ring of chromosomes would be formed as indicated in Fig. 118.

These ring formations are known as *catenations*. Many peculiar synaptic configurations can be explained by means of reciprocal translocations, for the homologous parts of chromosomes apparently attract each other at synapsis. Chains and other queer formations of the chromatin material also result from the attraction of homologous parts of chromosomes that through reciprocal translocation have come to occupy abnormal places.

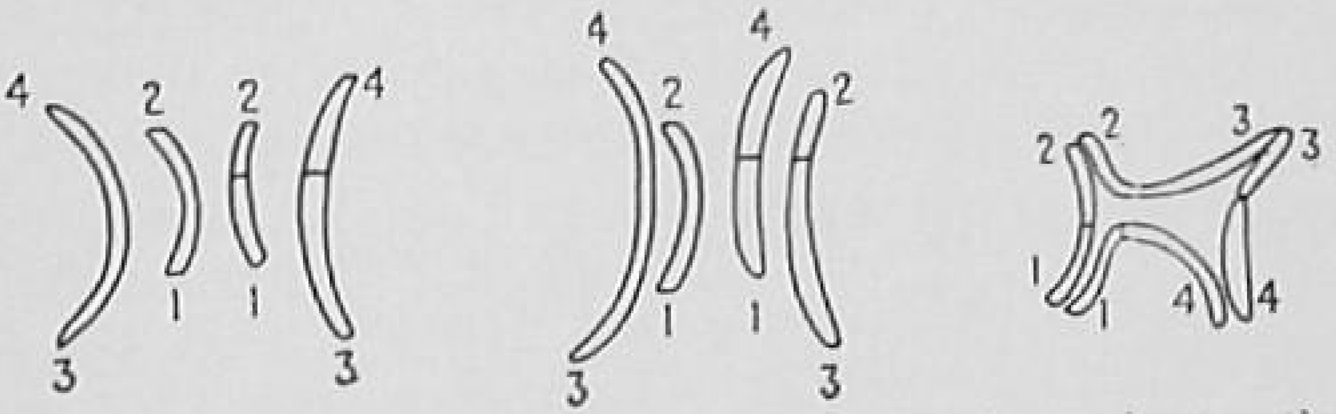


FIG. 118.—Diagram showing reciprocal translocation and catenation.

Since these abnormal formations of the chromosomes at synapsis are found in nature, many having been discovered by Blakeslee, Belling, and others in the Jimson weed (Datura), as well as being possible of creation by experimental treatment of plants through irradiation, it is assumed that they, along with all the other types of gene and chromosomal changes, are responsible for certain evolutionary changes. It has been shown for instance that the F_1 hybrid between a North and a South American species of Datura shows two circular formations of four chromosomes each, together with eight synapsing pairs. Painter's discovery of a similar amount of chromatin material in the rat and the mouse, although differently arranged, has furnished the basis for the belief that these two species have arisen from a common ancestor through translocations and gene mutations.[1]

The present wide complexity of the gene contents of the chromosomes must also be due in large measure to the translocations which have occurred in the past. For example, in Drosophila the numerous experiments have shown that genes producing reactions which control the same part of the body (such as the eye) may be located in different chromosomes. This may be due to ancient translocations which duplicated the genes for the particular character concerned. Later these would become differentiated from one another by changes in the genes, and we now find these similar genes in the different chromosomes all

[1] HURST, C. C., "The Mechanism of Creative Evolution," p. 81, The Macmillan Company, New York, 1932.

producing a reaction on the same part of the body. In this way the complexity of organisms must have been immensely increased, and it is evident that translocations giving rise to transmutations of chromosomes have played a great part in the general progress from lower to higher organisms which has taken place and they may be regarded as one of the prime factors in Creative Evolution.

Inversion.—Another type of chromosomal mutation is that called *inversion*. In this situation a portion of a chromosome has in some manner become inveretd. This might happen because a chromosome became looped upon itself and then failed to uncoil in the normal manner. This possibility is indicated in Fig. 119.

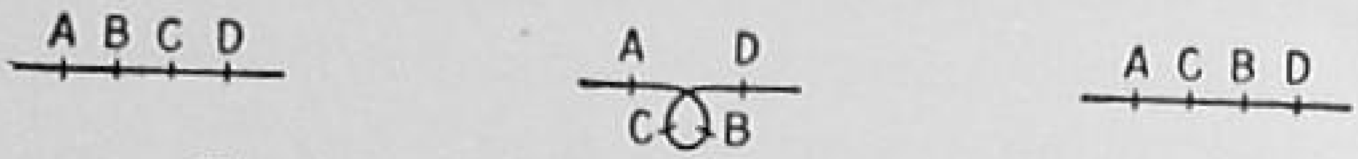


FIG. 119.—Diagram of process of inversion.

An instance of inversion is found in Drosophila. There are two species of Drosophila (*melanogaster* and *simulans*) that are interfertile, although the hybrids are sterile. Chromosome maps for both species have been constructed from the data of breeding experiments and these show that the genes are very similarly located in the two species in chromosomes I and IV. In chromosome II the genes so far studied appear to be in the same order although there are variations in the distances between genes in the two species. In chromosome III not only are there differences in the distances between genes but in about the middle of the chromosome in *D. simulans* a section has become completely inverted in comparison with *D. melanogaster*.

Deficiency.—Still another type of mutation is that known as *deficiency*. This arises from the loss or inactivation of a portion of chromosome, which is not lethal provided the deficiency is not too large and the organism is not homozygous for the deficiency. One of the best known examples of deficiency is that leading to the production of notched wings in Drosophila. Notch behaves as a dominant, is lethal when homozygous, and is located at about point 3 in the X chromosome.[1]

> A Notch female from a red-eyed stock crossed with a white male gives Notch and normal offspring as expected, but all the Notch flies show the recessive white eye (which is located at 1.5), as though the Notch female contained no wild-type allele of white. The normal-winged flies are all red-eyed. Similarly, the gene facet, at 3.0, showed this peculiar pseudodominance when crossed with Notch, and the gene Abnormal at 4.5 was also affected. Bridges and Mohr, who studied this condition, assumed that Notch was due to the absence of a piece of chromo-

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," 3d ed., pp. 233–234, McGraw-Hill Book Company, Inc., New York, 1939.

some in this case bearing the loci from white through Abnormal. This was called a deficiency and in conformity with the assumption, the map of the X in Notch is about four units shorter than normal. Much later the actual absence of this section of the chromosome in Notch females was proved by examination of the salivary gland chromosome.

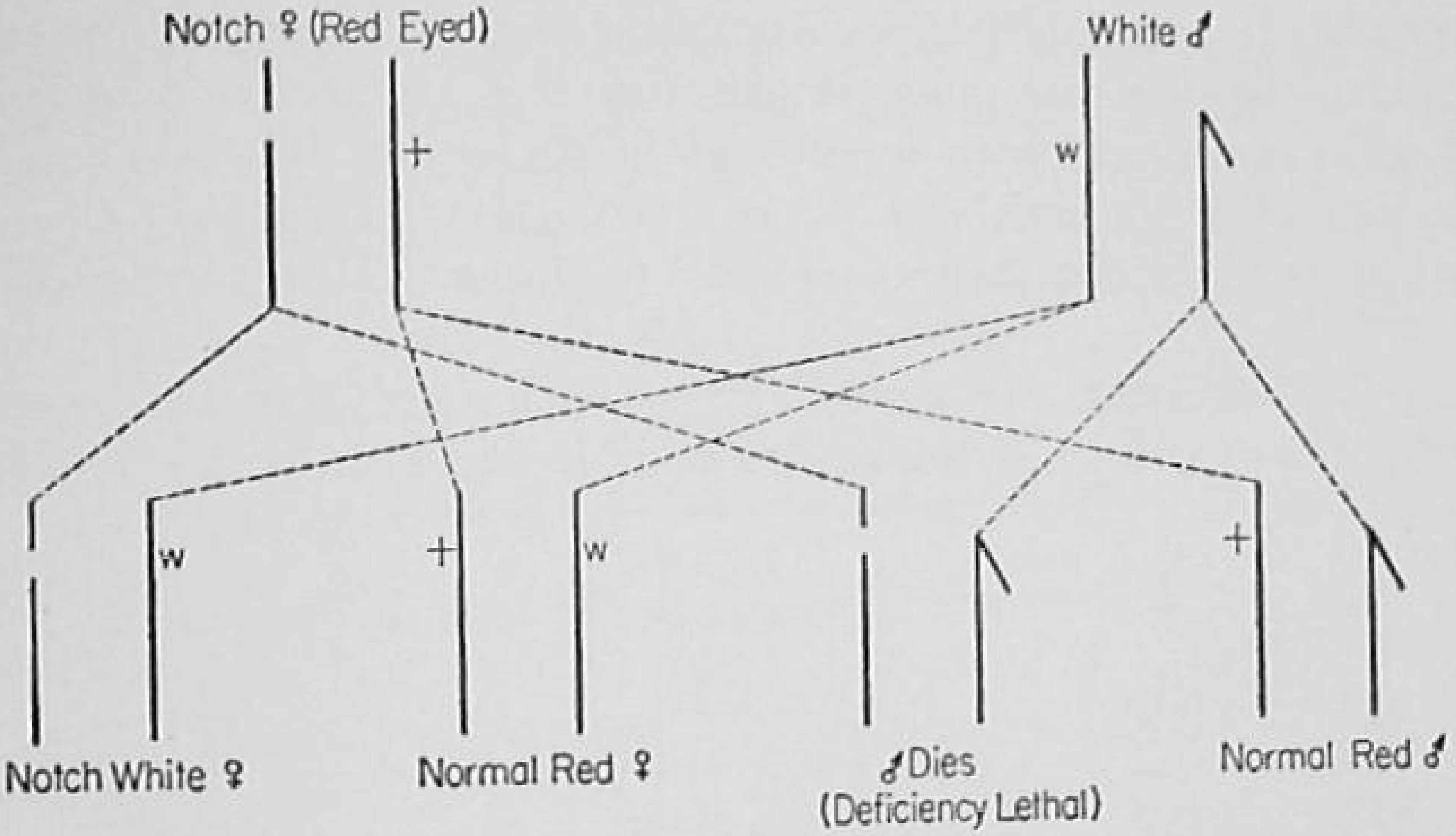


FIG. 120.—The inheritance of notch deficiency in *Drosophila melanogaster*. (*Sinnott and Dunn, Principles of Genetics.*)

Duplication.—We have seen in the previous section that a chromosome may become deficient or lacking in certain genes by a portion of a chromosome becoming lost. This might occur through unequal crossing over between two homologous chromosomes. If this happened, the unequal interchange, besides producing a deficient chromosome, would also give rise to a chromosome with some genes duplicated. This is illustrated in Fig. 121.

One of the above chromosomes is deficient for genes *B* and *C*, whereas the other has a double dose of these genes, *i.e.*, they are duplicated.

FIG. 121.—Diagram illustrating both deficiency and duplication due to unequal crossing over.

A chromosome fragment, however it arises, is known as a *duplication*, and it may exist by itself or become attached to some other chromosome.

One of the best known duplications is that of the bar eye pattern in Drosophila, long known as a dominant at point 57 in the X chromosome. Zeleny found that homozygous bar-eyed flies very occasionally produced normal round-eyed offspring and even less frequently the ultra- or double-bar pattern. By the use of other mutant genes close to bar, Sturtevant and Morgan showed these exceptions to be due to unequal

crossing over at the bar region, so that the normals showed a slight deficiency compared with bar and the double bar a duplication. Since the normal flies showed no actual deficiency, it was reasoned that bar was originally a duplication. These facts have been substantiated by Bridges's cytological study of the salivary-gland chromosomes, which shows bar to be a duplication. The further fact that the duplication in separate chromosomes produces bar, and that, when the duplication occurs in one chromosome, it produces double bar led Sturtevant to the conclusion that the position of the gene in the chromosome, as well as its nature, was influential in the final effect produced. This is the *position-effect* theory.

Duplications may also arise from crossing over between inverted portions of two chromosomes as illustrated in Fig. 122.

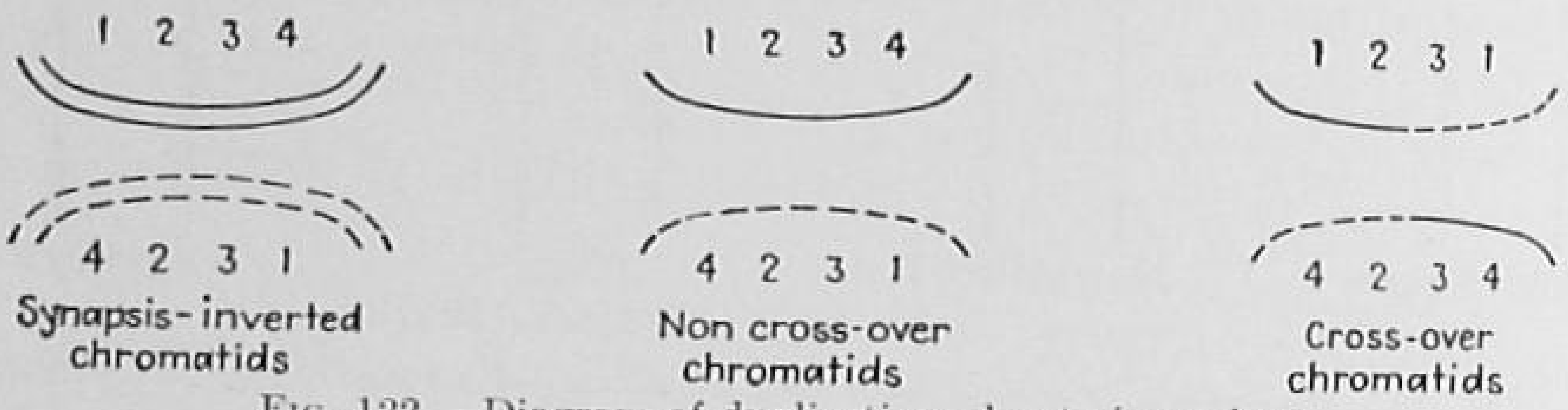


FIG. 122.—Diagram of duplications due to inversions.

Heteroploidy.—A new organism generally arises from the union of an egg and a sperm in each of which the number of chromosomes has been reduced to the half or haploid number (n). The coming together of these two half numbers at fertilization again restores the chromosomes to the diploid number ($2n$). Sometimes a new organism gets one (rarely two) too many or one too few chromosomes and is therefore $2n + 1$ or $2n - 1$. Many of these are viable and have been studied both genetically and cytologically. These individuals differ slightly from the wild type in appearance and are often less viable, less fertile, and do not breed true.

In Drosophila, forms are known that lack one member of the small IV pair of chromosomes. Such a fly with only one IV chromosome is called a *haplo*-IV fly, and one with an extra IV chromosome is called a *triplo*-IV fly. These individuals, with any greater or smaller number of chromosomes than the normal for the species, vary from the normal to a greater or less extent. In other words, the normal number of chromosomes is necessary for the production of a "normal" individual, though this does not mean that those individuals not having the normal number of chromosomes will necessarily be unable to survive and leave offspring.

Triplo-IV Drosophila have narrow, pointed wings, smooth eyes, course bristles. When crossed with eyeless, they give ½ triplos: ½ wild type. These triplo F_1 flies crossed back to eyeless give 5 wild type: 1 eye-

less. Nondisjunction of the two X chromosomes, discovered by Bridges, produces another form of heteroploidy. White-eyed females crossed with red-eyed males should yield red-eyed females and white-eyed males but occasionally do just the opposite owing to nondisjunction of the X chromosomes following synapsis.

In the Jimson weed, which has 12 pairs of chromosomes, Blakeslee, Belling, and their coworkers have discovered many types of heteroploids. Any one chromosome present in a triple dose gives what is termed a *primary heteroploid*. All the possible 12 primaries have been studied, and each of them has a characteristic mutant appearance. Another type with the extra chromosome made up of parts of two homologous chromosomes rather than being just an additional whole chromosome is called a *secondary heteroploid*, and still another type with the extra chromosome made up of parts of two heterologous chromosomes is called a *tertiary heteroploid*. These latter two types give many peculiar ring formations of the chromosomes at synapsis.

In the evening primrose (Oenothera), in which the diploid number of chromosomes is 14, the following number of chromosomes, according to Gates, have been reported: 15, 20, 21, 23, 27, 28, 29, 30. Those with other than 14 chromosomes have definitely distinguishing somatic characters, which indicates again that the characters are under the control of the genes.

Haploidy.—The haploid condition is normal in some species that reproduce parthenogenetically, *e.g.*, bees, wasps, some moths, and rotifers. A few other species can be made to reproduce parthenogenetically by artificial means, *e.g.*, certain amphibians. This has recently been accomplished by Pincus in the rabbit with the probable early restoration of the diploid condition in the embryo by means of division of the chromosomes without subsequent division of the cell. Artificial haploids are generally small and lacking in vigor and very rarely produce viable gametes. Where viable germ cells are produced, they are undoubtedly the result of meiosis without reduction. Haploids can be induced by various environmental means such as cold and irradiation.

Polyploidy.—Forms with some multiple of the haploid number other than two are called *polyploids*. The most frequent ones found are triploids ($3n$) and tetraploids ($4n$), with occasionally pentaploids, hexaploids, and octoploids appearing. Polyploids are known in many plants, *e.g.*, Datura, Oenothera, tomatoes, and some mosses, and in a few of the lower animal forms, including Drosophila. They probably arise naturally through failure of the germ cells to divide after the nuclear material has divided. They can also be induced artificially by various environmental agencies, and recently a method for inducing polyploids

in plants through the use of colchicine has been developed. Polyploids have a commercial as well as scientific interest, because the plants and fruits are generally larger, heavier bearing, and more vigorous.

Triploids generally result from the crossing of diploid and tetraploid parents. Reproduction by these forms is, as expected, very irregular, for the three sets of chromosomes assort at random into all possible combinations, thus giving very few functional germ cells.

Tetraploids are of two sorts. Those which arise within one species are called *autotetraploids*. These reproduce approximately normally, for the four members of each set of chromosomes come together at synapsis forming a quadrivalent from which two of the homologues pass at random to each gamete. A cross of a purple-flowered tetraploid Datura (*PP PP*) and a white-flowered (*pp pp*) gives a purple F_1 (*PP pp*) and an F_2 ratio of 35 purple: 1 white, for the gametes forming at random will be 1 *PP*, 4 *Pp*, and 1 *pp*.

Tetraploids formed by crosses between two species or genera, with subsequent doubling of each parental set of chromosomes to form a tetraploid, are called *allotetraploids*. One of these was reported by Karpechenko in 1928. It resulted from a successful cross between the radish and cabbage. The haploid number in each of these species is 9, so that the F_1 hybrid had 18 chromosomes. These hybrids produced a few seed, enabling an F_2 to be produced. Some of these F_2 plants resembled the hybrid and on examination were found to contain 36 chromosomes. Study of the meiotic divisions of the F_1 showed 18 univalents, indicating that no pairing had taken place between the radish and cabbage chromosomes. It is assumed that the F_2 resulted from the union of gametes with the combined chromosome make-up. The F_2 were evidently tetraploids with 18 radish and 18 cabbage chromosomes. These plants were fertile and bred true, each transmitting 9 radish and 9 cabbage chromosomes through each germ cell. This intergeneric hybrid is a new, fertile species that cannot be crossed back on either parent. It demonstrates that new species can arise from species or genera crosses. It is, in effect, evolution at work.

If any change in the gene complex or in the distribution of chromosomes arises in the egg or sperm that are to give rise to the new individual, in the developing embryo previous to the laying down of the germ plasm in its testicles or ovaries, or in the viable germ cells produced by the individual after sexual maturity, variations will result in the offspring which may be heritable. Aberrations in the distribution of chromosomes may occur at any of the millions of cell divisions that must intervene between the zygote and the completely developed individual. Many such aberrations are known. This means, of course,

that any animal may, under certain conditions, transmit characteristics which he (or she) does not exhibit and may not transmit characteristics which he (or she) does exhibit.

Mutations and freaks should not be confused. A mutation is a sudden germinal variation that breeds true. A freak is probably a sudden somatic variation, such as a two-headed calf, a six-legged pig, and many others that may be seen at the circus but which will not breed true. The freak has no genetic value, and, although the mutation may not have value, if often does, and, because of the fact that it breeds true, the characteristic may be perpetuated.

Breeding Systems and Variation.—It is obvious from the foregoing that genetic variation is dependent on what transpires in the genes and chromosomes. In addition to these gene or chromosome changes, however, there is the further consideration of the sorting out of the whole genetic material into different sorts of combinations. Self-fertilizing plants tend to separate themselves into homozygous forms. If one of these plants were *Aa*, its offspring would be ¼ *AA*, ²⁄₄ *Aa*, ¼ *aa*. Continued selfing would constantly change the proportion of the genotypes according to the formula $2^n - 1\,AA{:}2\,Aa{:}2^n - 1\,aa$, where n is the number of generations of self-fertilization. In other words, about one-half the heterozygous gene combinations become homozygous each generation the inbreeding is continued. This is true for every pair of heterozygous genes that the original parent might have possessed. Even with 15 pairs of heterozygous genes, practically all of them will have been separated out into homozygous forms by 10 generations of selfing. There would, of course, be many combinations of these 15 pairs of genes, but they would all be sorting out into homozygous forms. With two pairs of genes, *Aa Bb*, we would be getting *AA BB*, *AA bb*, *aa BB*, and *aa bb* forms, or 2^2. With 15 pairs of genes, we would get 2^{15} different forms. Selfing is of course the closest sort of inbreeding possible. It should be noted that, granted equal viability, the number of recessive and dominant genes in the population remains the same.

Inbreeding, therefore, is seen to have a direct effect on variation. When it is practiced, the population tends to increase in variability by becoming broken up into many separate, though highly uniform, families or strains. This, of course, offers greater opportunities for selection within desirable uniform lines, and, when this sort of selection is practiced, the population becomes more uniform, owing to the selection, however, rather than the inbreeding.

In the higher animals, however, selfing is not possible because the union of an egg and a sperm produced by two separate individuals is necessary to produce a new individual. If we start with the animals

Aa and Aa and their offspring interbreed freely, the population will become $\frac{1}{4}$ AA, $\frac{1}{2}$ Aa, and $\frac{1}{4}$ aa. The recessive gene is again, granted equal viability, just as numerous as the dominant and does not tend to become obliterated unless it has a lower survival value or unless selection is practiced against it. Whatever the original proportion of the two genes is, the mechanism of inheritance tends, in a freely breeding large population, to maintain this proportion. If we let q represent the original proportion of A, and $1 - q$ the original proportion of a, then in any succeeding generation the proportions of the homo- and heterozygotes will be $q^2\ AA : 2q(1 - q)\ Aa : (1 - q)^2\ aa$.

If we knew that 1 per cent of Holstein calves were the recessive red (aa), then we would also know that 81 per cent were homozygous black (AA) and 18 per cent heterozygous (Aa), because, if $(1 - q)^2 = 0.01$, then $(1 - q) = 0.1$, and, since the whole population is unity, or 1, then q must equal 0.9 and q^2 0.81 and $2q(1 - q) = 0.18$. If inbreeding were practiced in this population, the proportion of homozygotes would of course be increased at the expense of the heterozygotes.

The above discussion of genetic equilibrium applies only to very large populations. In small populations, however, the mechanism of inheritance tends to reduce variation by eliminating certain genes at the same time that it is fixing others in a homozygous state.

Nicking.—If offspring of certain matings are of a high order of excellence and in general better than their parents, then breeders say they "nicked" well. It sometimes happens that the mating of two average animals results in the production of an outstanding individual from the standpoint of type, performance, or both. This effect may, of course, be largely due to environment. It may, on the other hand, be due to inheritance. Possibly each parent was lacking in certain genes that would make for excellence although possessing a great many of the necessary genes. If the two parents lacked in different genes, the offspring might get a full complement, some from each parent. Crosses of white-eyed and eyeless Drosophila result in normal red-eyed offspring. One parent is recessive for a pair of genes making the eyes white, though it has the normal genes for presence of eyes. The other parent is recessive for the genes for presence of eyes but has the normal genes for red eyes. When mated, each parent supplies what the other lacked, thus giving normal red eyes.

It must be remembered, however, that these offspring are heterozygous and cannot breed true. Sometimes the argument that geniuses do not always beget geniuses is used against the chromosomal theory of inheritance. If, however, the genius arose as did the red-eyed flies just mentioned, we would not necessarily expect him to beget geniuses, so

that in place of refuting the theory of inheritance, facts such as these tend to substantiate it. When favorable "nicks" arise, their breeding ability must receive careful scrunity before they are approved, because it is possible that their diverse origins will be manifest in their offspring.

Prepotency.—The term *prepotency* is often used in rather a loose fashion and is applied generally to males. It is usually thought to be associated with the general characteristic of vigor. That is, it is applied very often to an outstandingly vigorous male. The term really means the ability of an animal, male or female, to stamp its own characteristics on its offspring. For instance, the Hereford bulls used on the grade cattle of the range generally put white faces on all the offspring of such matings. If a Hereford-Angus cross is made, however, a white-faced black-bodied[1] polled individual is produced, and the question arises as to which animal is prepotent. Some will say the Hereford because of the white face on the offspring. Others will say the Angus because of the polled characteristic and black body. The truth is, however, that one is not justified in speaking of either animal as being prepotent. The animal is not prepotent; the various characteristics that the animal may exhibit may or may not be prepotent. In this case, polledness of the Angus, white face of the Hereford, and black body color of the Angus is each prepotent. The same results would be secured no matter which one of the breeds in the above cross was selected as the male and which one as the female and also regardless of vigor. Graphically the results in regard to these three characters and with the dominant characters italicized might be represented as follows:

PP polled *ww* black face *BB black body* } Angus	*pp* horned *WW white face* *bb* red body } Hereford

→ *PwB* *pWb* ←

PpWwBb

polled, white-faced, black-bodied crossbred

It is not enough, however, to say that certain characters are prepotent. When the above crossbred produces spermatozoa or ova, as the case may be, the factors will separate and recombine into all the possible combinations, reduction taking place at the same time, so that ova or spermatozoa of the following make-up are produced: *PWB*, *PWb*, *PwB*, *Pwb*, *pWB*, *pwB*, *pWb*, *pwb*. If one of the above crossbreds is mated to a Hereford pure for horns, white face, and red body, or

[1] The Angus might be heterozygous for color and therefore give rise to a red-bodied calf.

pp WW bb, and hence capable of producing only *pWb* spermatozoa or ova, calves will result 50 per cent of which will be horned and 50 per cent of which will be red-bodied. Thus, the characters which are fully prepotent in the purebred, *viz.*, polledness and black body, cease to be fully prepotent in the crossbred, because the crossbred produces more than one kind of reproductive cell, actually producing eight different kinds as to these three characteristics of horns, face color, and body color. The above characters are simple in their nature, being controlled specifically by one factor, although many other factors may be involved. According to Wright:

> Most characteristics probably depend on a large number of hereditary units, but nevertheless the nature of prepotency is believed to be essentially the same. So far as there is prepotency, it is a property of characteristics (or really of the hereditary units back of the characteristics), not of individuals, breeds, or sexes, and whatever the characteristics, there can be no prepotency unless the individual produces only one kind of reproductive cell so far as it is concerned.

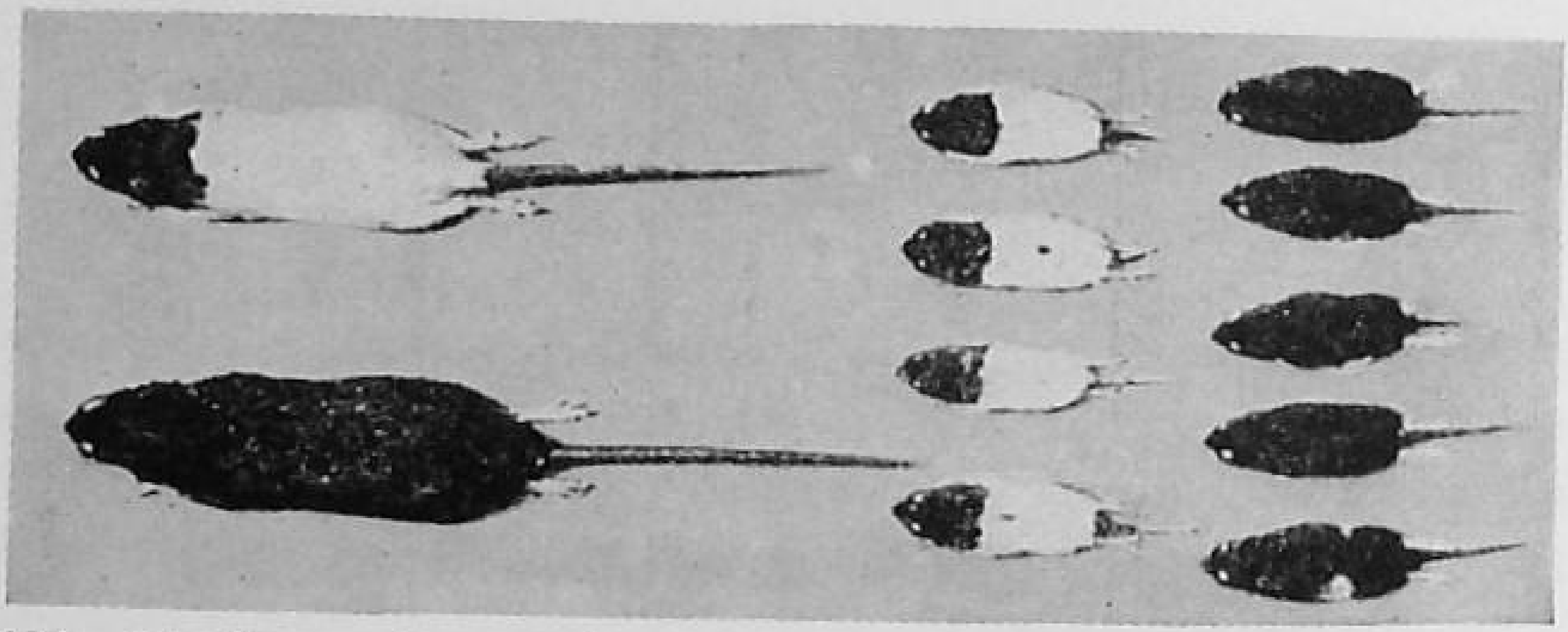


FIG. 123.—Inheritance of a recessive pattern of white spotting seen in "hooded" rats. The parents (*left*) are a homozygous hooded mother and a heterozygous "Irish" father (black with white belly). An entire litter of their young is shown at the right. Four are homozygous hooded like the mother, five are heterozygotes like the father. Note fluctuation in both classes. Such fluctuations are found to be in part heritable. (*From Castle, Genetics and Eugenics, Harvard University Press.*)

Technically, prepotency depends upon the character being dominant and the individual being homozygous; *i.e.*, the individual must carry *AA* in its chromosomes, not *Aa* or *aa*. The more prepotent an individual is, the less the probability of variation, good or bad.

A prepotent animal will have offspring that closely resemble it, but whether or not these offspring are themselves prepotent will depend on what genes they got from their other parent. If they have many homozygous dominant genes, they will be prepotent. An animal is seen, therefore, to be unable to transmit its own prepotency because it contributes but one-half of its total inheritance to any of its offspring.

Variation Guided by Selection.—Although it may be questioned whether selecting animals with a definite end in view can specifically

be said to cause variations in that direction, it is, nevertheless, true that one variation in a given direction seems to make other variations in that direction more probable. Thus it is well known that by selecting in Holsteins or Ayrshires the proportion of pigmented to nonpigmented area may be shifted from one of almost entire pigmentation to one almost white. Likewise, in Herefords, the white of the face, which behaves as a unit in inheritance, may be increased or decreased in area. Functional variations, such as speed in horses, milk production in cattle, wool production in sheep, etc., can also be guided by selection—in fact, it has been selection, both natural and artificial, that has given rise to most varieties and perhaps species. Castle states[1] as an interpretation of factorial behavior in such selection:

Many students of genetics at present regard unit-characters as unchangeable. They consider them as impossible of modification as are the atoms. To recall Bateson's comparison, the carbon and oxygen of carbon monoxide, CO, are each

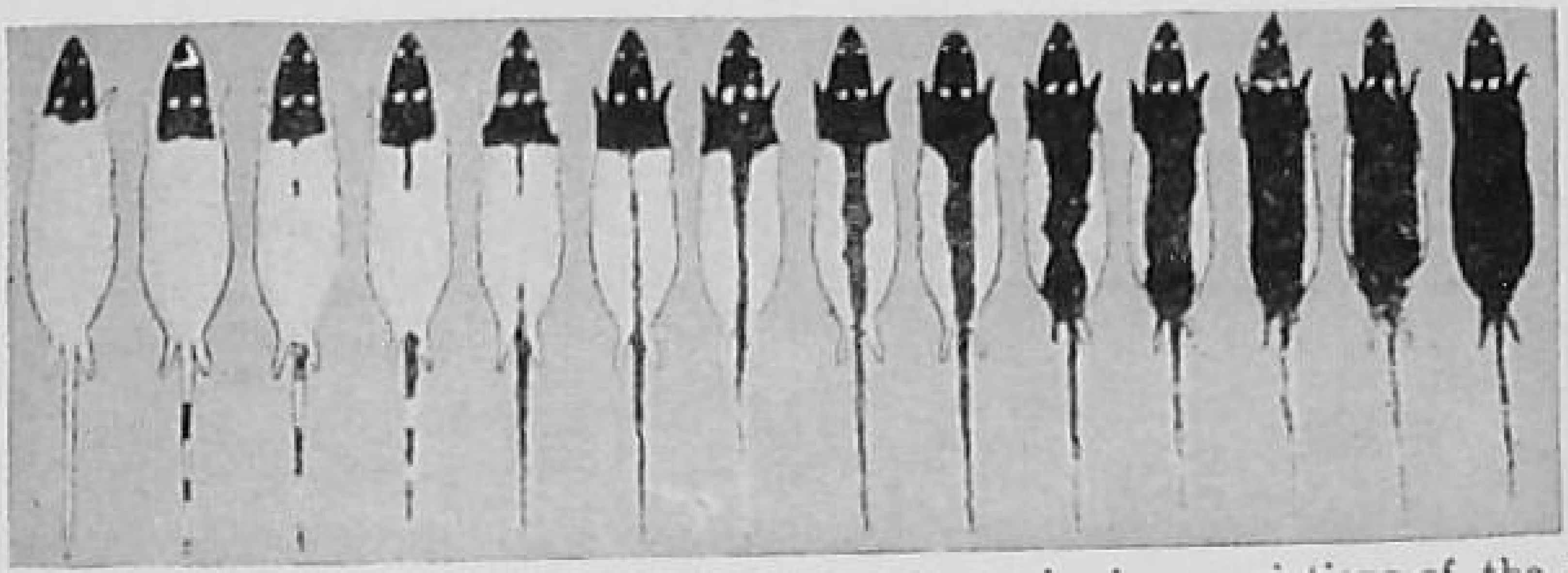


Fig. 124.—A series of grades for classifying the plus and minus variations of the white spotting pattern of hooded rats. (*From Castle, Genetics and Eugenics, Harvard University Press.*)

unchangeable. Adding another atom of oxygen does not alter them, though it changes radically the compound formed which becomes carbon dioxide, CO_2, possessed of very different properties. But the carbon and the oxygen are still there unaltered and recoverable. This question is one of great practical importance—are unit-characters as constant as atoms, so that we can merely recombine them, or are they different in nature from atoms so that we can modify as well as recombine them. Much careful work has been devoted to the solution of this question. It was at first assumed from chemical analogy that characters which behave as units in heredity must, like C and O in the case of carbon dioxide, emerge from combinations unmodified. But presently case after case came to light in which this was not true. Albinism emerged from crosses tainted with color; clear yellows emerged from crosses intensified to red, or diluted to cream, or sooty with minute quantities of black; patterns such as are seen in Dutch or in English rabbits, or in hooded rats, emerged considerably altered in appearance.

[1] Castle, W. E., "Genetics and Eugenics," pp. 237–240, Harvard University Press, Cambridge, Mass., 1930. (Reprinted by permission of the President and Fellows of Harvard College.)

Facts such as these were interpreted in two different ways. It was assumed by some that the actual unit-character, factor, or gene involved was subject to quantitative and possibly to qualitative change. By others it was assumed that the observed character changes were not due to changes in single genes but to the supplemental or modifying action of the other genes.

Hooded Rats and Selection.—As a test of these rival interpretations, we may discuss a typical case. The hooded pattern of rats clearly behaves as a simple unit-character allelomorphic to Irish pattern or to self in crosses. But the hooded pattern as seen either in pure-bred or in cross-bred litters of young varies slightly, and such variations have a genetic basis since by selecting either the whitest or the blackest individuals, one can either whiten or blacken the average racial condition. Races corresponding with the extremes of the series shown in Fig. 124 were thus produced. The question now arose whether the observed changes had occurred as a result of change in the single unit-character or gene clearly concerned in the case, or whether this was due to other agencies. To test the matter the selected races, now modified genetically in opposite directions, were crossed repeatedly with a non-hooded (wild) race. The recessive hooded character disappeared in F_1 but was recovered again in F_2 in the expected 25 per cent of this generation. These extracted hooded individuals, following each cross, were less divergent than their hooded grandparents from the ordinary hooded pattern. After three successive crosses (six generations) the whitest individuals extracted from the dark hooded race were no darker than the darkest individuals extracted from the white hooded race. In other words repeated crossing with the non-hooded (wild) race had caused the changes in the hooded character, which had been secured by selection, largely to disappear. The conclusion was drawn that the hooded allelomorph itself had remained unchanged throughout the selection experiment, and that the phenotype had been altered by associating with the hooded gene a different assortment of other genes in each of the selected races, these serving as genetic modifiers. In the course of the selection experiment a mutation was observed to occur in the plus series to practically the Irish stage. This is not included in the summary but is mentioned to show how it is possible for selection to be aided in its progress by the occurrence of contemporaneous genetic changes, no less than by the sorting out of variations originally present in the foundation stock. Apart from the mutation mentioned the results of selection in this case show conclusively that the changes obtained had not occurred in the gene for the hooded pattern, but in the residual heredity. Other cases of apparent gradual change in unit-characters under the action of selection may be explained in a similar way. Accordingly, we are led to conclude that unit-characters or genes are remarkably constant and that when they seem to change as a result of hybridization or of selection unattended by hybridization, the changes are rather in the total complex of factors concerned in heredity than in single genes.

Types and Frequency of Variation.—All animals will produce variations to a greater or less degree, depending upon the interaction of a great many factors. Sometimes extremely valuable animals arise from

the mating of mediocre parents. Such variates should be studied carefully as to their ability to transmit their own desirable features, and nothing along this line should be taken for granted. Of decidedly more value than the animal that produces one such outstanding individual and a host of inferior ones is the animal that has a tendency to beget a uniform lot of offspring better than the preceding generation, even if the increase in excellence is small in each individual.

Innumerable instances could be cited of full brothers that are evidently genetically unlike, because their offspring are very unlike. The same is true of full sisters; *e.g.*, in cattle, one sister is often vastly superior to another in milk production. It is quite evident, therefore, that variation is a very potent and ever-present force molding new forms both anatomically and physiologically, and that its mechanism is to be sought in the genes and chromosomes, their interactions with each other, and their potentiality for individual change.

Summary.—We have seen in this chapter that the genes and chromosomes may undergo a great variety of changes. As we would expect, such gene or chromosomal changes tend to be hereditary, for the genes and chromosomes are the actual mechanism of inheritance. The breeders' raw material for fashioning finer animals is variation. He must determine what the cause of the variation is and so plan his breeding operations to conserve the good and weed out the bad variations. He does this largely by selection and systems of breeding. Genetic variation is a complex mechanism and is made more difficult by the effects of various types of dominance and epistasis as well as by the fact that most characters are more or less elastic under different environmental influences. An understanding of the underlying mechanism of variation makes us more cognizant of the inherent difficulties involved as well as more confident of ultimate success when our understanding of principles is fully mature.

References[1]

[1] See lists at end of Chaps. XI and XII.

CHAPTER XVI

THE PRINCIPLES OF VARIATION (*Continued*)

As stated in the previous chapter, there are two sorts of variation, genetic and somatic. We have seen that any changes in the genes or chromosomes may be inherited, because the genes and chromosomes from the parents form the actual "bridge of inheritance" between any individual and all of its millions of ancestors. We also learned that variations might be due to internal or to external stimuli. In this chapter we shall be concerned primarily with somatic variations that are generally caused by external stimuli, or, in other words, by the environment.

It seems almost certain that early in the evolutionary process the environment must have wielded a marked influence on the simple forms of life and caused their germ plasms to vary in different ways. Experimentally, this is possible in plants and lower animal forms today. In the higher animals, however, with their various adaptations for protecting the delicate germ cells, the possibility or extent of such external influences is much lessened. Parallel induction (same influence affecting both soma- and germ plasm) in the cases of alcohol or lead poisoning must be admitted, but here the effect appears to be temporary.

Environment and Somatic Variation.—Among the effective external stimuli are light, temperature, food, moisture, and other influences tending to make the organism deviate from its normal as specified by the make-up of the germ plasm that gave rise to it. As pointed out by Babcock and Clausen, external stimuli may affect the development of characters in three ways.

1. They may modify the development of inherited characters; *e.g.*, red, white, or blue light causes marked variations in the showy Sedum, even though the several plants be of the same genetic make-up. Temperature affects the degree of pigmentation in moths and butterflies. Food supply affects the relative size of body parts of Hyalodophina, a crustacean. Moisture affects the plumage color of pigeons.

2. They actually condition the production of characters whose hereditary determiners are present in the germ plasm. For example, light conditions normal development in plants. Temperature, when low, causes red flowers in the Chinese primrose, when high, induces white

flowers. The kind of food supplied to the larvae of bees determines whether the females shall be fertile (queen bees) or infertile (workers). Moisture concentration brings about development of abnormalities in black banding on the abdomen of Drosophila, a fruit fly.

3. They may cause germinal variations that result in the appearance of new heritable characters.

Modifications may be impressed on the soma from the outside; genetic variations are expressed from the inside, specifically from the germ plasm. The latter are heritable, whereas modifications seem to be nonheritable. If it is possible to modify the function of any organism in a given way, it must be because the organism inherited the ability to react in such a way. This does not necessarily mean that offspring from such an individual would necessarily show the same aptitude to modification. That would depend on the genetic make-up of the individual in question. The possible effect of amphimixis, or the bringing together of two diverse bits of germ plasm, must also be taken into consideration. Animals of a good strain that are themselves stunted and not developed to the limit of their inherent capacities may beget offspring of a type capable of great development. Daughters of scrub cows, developed under an environment tending toward full development of capabilities, produced 13 per cent more milk and 12 per cent more butterfat than their scrub dams of the same type of breeding, which had been developed under less favorable conditions.

It is the province of animal breeders to develop fully all the capabilities that their animals possess. Not that these so-called "modifications" will necessarily be inherited, but, if the parents exhibit favorable modifications, it must be because they carry that particular type of germ plasm, and, unless they are extremely heterozygous or amphimixis interferes, the offspring of such parents should in general exhibit like capabilities. Modification is an aid to selection but like all other aids must subject itself to the breeding test.

Acquired Characters.—The inheritance of acquired characters has been called "one of the historic battle grounds of biology." The animal breeder is vitally interested in the solution of the question of the inheritance of acquired characters. The successful breeder seeks to develop for himself and to leave to posterity a better type of animal than the one with which he was supplied at the beginning. It is perfectly natural for him to hope, and perhaps believe, that any increase in quantity or quality of produce he can bring about will be cumulative in his animals.

Before proceeding to a discussion of the evidence pro and con, it is essential to define specifically what is meant by an acquired character. Shull defines acquired characters as "those modifications of bodily

structure or habit which are impressed upon the organism during its individual life." As Thompson has stated it, the precise question at issue is this: "Can a structural change in the body, induced by some change in use or disuse or by a change in surrounding influence, affect the germ cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree, the modifications which the parent acquired?"

Any one of the higher organisms is the result of the union of a certain spermatozoon with a certain ovum. The chromosomal content of the particular spermatozoon and of the ovum that have united to produce any given individual determines the normal characteristics for this individual. With normal nutriment and a normal environment the individual will approximate its own norm as specified through its inheritance. Now both the anatomy and physiology of the organism are

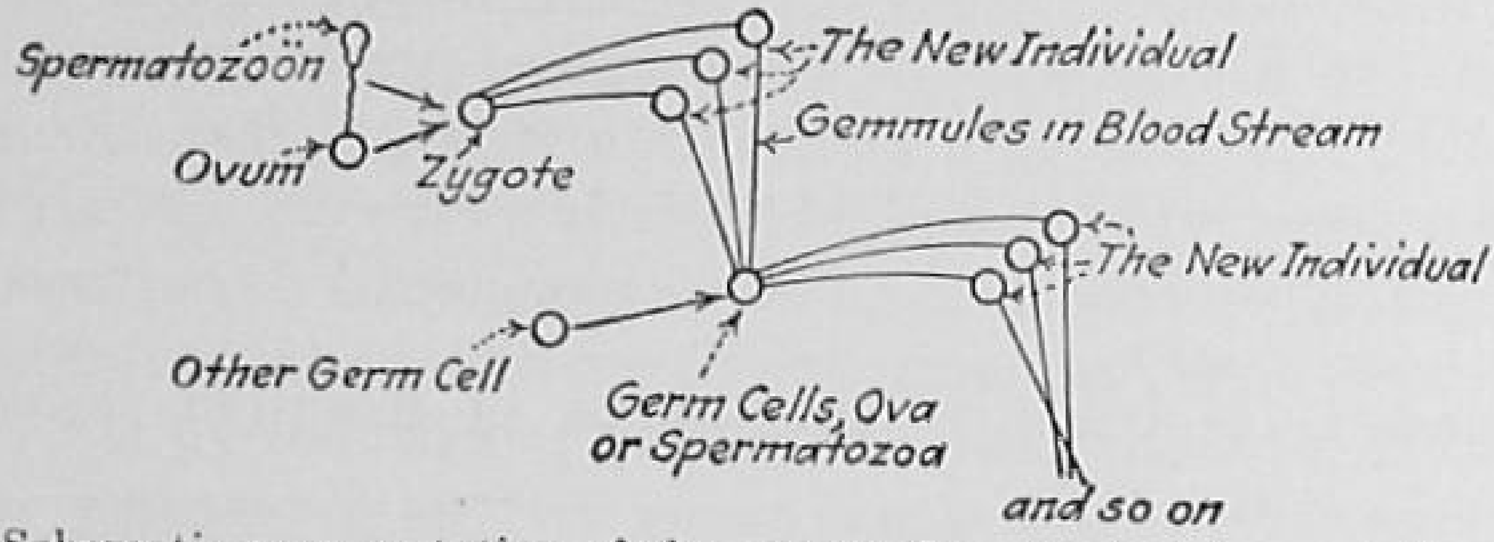


FIG. 125.—Schematic representation of the supposed method of transmission of acquired characters.

perfectly capable of modification, and the precise question at issue is whether or not such bodily modifications will be impressed upon the germ cells and thus become a part of inheritance.

In an evolutionary sense all the characteristics that present-day organisms exhibit have been acquired, for evolution teaches that life originated in a very simple form and that it has gradually grown more complex—in other words, has ever continued to evidence new characteristics. Even this, however, is far from proof that changes in the somatic cells caused changes in the germ cells. May not the reverse of the last statement be the truth of the matter? Aligning cause and effect into their true relationship is not always an easy thing to do.

Lamarckism vs. Weismannism.—Lamarck, a French scientist, and Darwin, the famous English author of "The Origin of Species," believed that acquired characters could be inherited, and for a mechanism it was postulated that the blood stream which bathes all parts of the body would have something (gemmules) put into it by the part affected or by the character acquired and that the blood, later flowing to testicles and ovaries, would deposit this something in the ova or spermatozoa

and thus bring about the development of the character in the offspring. This is the theory of pangenesis.

Weismann has been the chief antagonist of the theory of the inheritance of acquired characters, and he also developed the idea of the continuity of the germ plasm. Under this conception the germ cells that any individual produces are thought of as arising, as do all the other cells of this individual, from the original zygote. Under this view the type of germ cell produced is dependent on the nature of the original zygote and is not affected by the soma or body that has also arisen from the original zygote. The accompanying diagrams should make clear the differing features of these two systems.

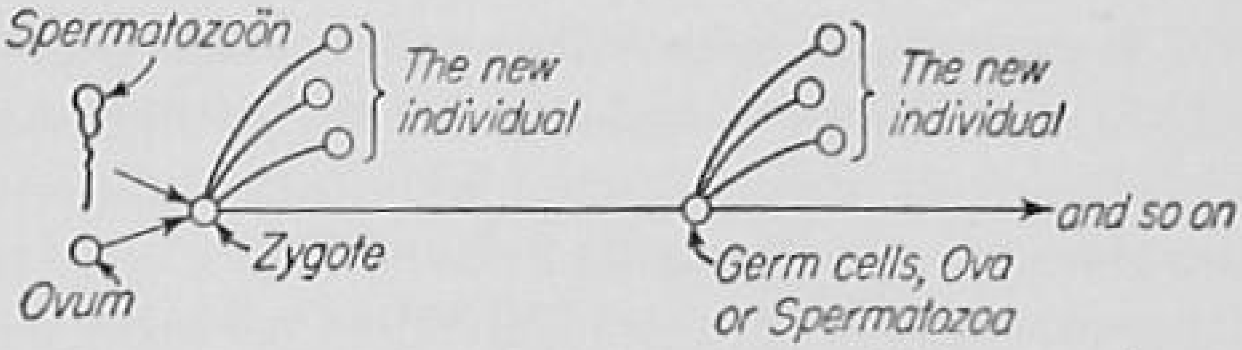


FIG. 126.—Schematic representation of the continuity of the germ plasm. The drawing also illustrates the fact that germ cells arise from previous germ cells rather than from present somatoplasm.

Requirements for Proof of Inheritance of Acquired Characters.—Babcock and Clausen say:

To satisfy the rigid requirements of an experimental proof any evidence of the inheritance of acquired characters must fulfill the following conditions:

First, a specific character or modification in the body or soma must be impressed upon the organism by a known factor in its environment or in its exercise of bodily function.

Second, the character or modification must be new. There must be no question of the reappearance of ancestral traits or characters, or of the specific relation of the determining factor to the character or modification in question.

Finally, the induced change in the organism must reappear to some, though not necessarily to its full degree in succeeding generations in the absence of the original factor which determined its production. Other conditions in the life of an offspring must remain unchanged.

The problem of the inheritance of acquired characters can be conveniently divided into the five following categories: (1) anatomical modifications, (2) environmental modifications, (3) functional modifications, (4) pathological modifications, and (5) psychological modifications.

Anatomical Modifications.—There are abundant data relating to mutilations. When the tail of a sheep is docked the sheep has acquired a character during its individual development, *viz.*, taillessness. It is also recognized at once that this characteristic is not passed on to descendants

of this sheep, but in succeeding generations it will be necessary to dock the lambs notwithstanding the fact that docking has been practiced for hundreds or thousands of generations. In this category come also the clipping of the horns of cattle, docking of horses' tails, clipping of dogs' ears and tails, etc. In none of these cases is the acquired character continued in the offspring. In the human family, there might be mentioned circumcision, which has been practiced for thousands of years, and also the binding of feet to prevent their full development practiced by Chinese women. Here, no more than in the cases cited of farm animals, is there found evidence that these acquired characters are being inherited in even the slightest degree.

Weismann in order to test this hypothesis cut off the tails of mice for 19 generations in succession and secured no shortening of the tails or absence of tails in any of the descendants. As Walter remarks: "It is a good thing that children of warriors do not inherit their parents' honorable scars of battle else we would have long since been a race of cripples." The same author also remarks in this regard that "evidently wooden legs are not inherited but wooden heads are."

Environmental Modifications.—The second category is that of environmental effects. Examples from both the plant and animal kingdoms can be cited. Capsella, a wayside weed, has gradually climbed to a mountainous habitat. As it climbed it "acquired" a dwarf character—at least it grows luxuriantly in the valley and is small, compact, and dwarfed in its mountain home, and, when taken back to the valley, continues in its dwarf characteristics. This can just as well, if not more logically, be explained by saying that those plants germinally constituted so that they grew somewhat dwarf would, for that reason, have a better chance of surviving under the more rigorous conditions and decreased food supply that prevail in an ever-increasing degree as the mountains are ascended. In other words, the force bringing about the change was not the inheritance of acquired characters, but "natural selection," which no doubt always has and always will, provided man does not interfere, weed out those types and individuals poorly fitted for their environment and preserve and prosper those better fitted to survive under the existing conditions.

Another example is the wind-lashed trees of our sea coasts, with all the branches growing out on the land side and pointing landward, but it is not known that seed from such trees would produce trees with that peculiar habit of growth if the trees were grown where the almost steady sea breezes did not blow. The case of the persistent sunburn of white men long resident in India might also be mentioned, but this "acquired characteristic" fails to reappear in their children born in England.

Ponies inhabiting the Shetland Islands are dwarfed because of the harsh climatic conditions and resultant scanty food supply. If brought to America's corn belt, such animals would no doubt give rise to offspring that would greatly excel them in size. Now, if these larger offspring, after reaching maturity, are returned to the Shetland Islands, will they continue to produce offspring that will attain large size? It is very unlikely that they will, and, even though they did, natural selection would give as logical and perhaps a more reasonable explanation than the inheritance of acquired characters could muster.

Functional Modifications.—The third category relates to inheritance of functional modifications due to use and disuse of parts. From a practical standpoint, along with the inheritance of disease, this probably furnishes the most interesting phase of the subject. It will be well at this point to examine critically just what is meant by acquired characters. Is the term more or less a misnomer? If so, would it not account for much of the loose thinking and arguing over the much-debated question? As Davenport suggests, the differences between animals in a given species are differences of degree and not of kind—they are quantitative and not qualitative. Horses show horse characteristics and not rabbit characteristics, except as both have certain general characteristics in common; cattle show characteristics of the cattle family and not those of the swine family, except as they have certain ones in common. Horses have draft power or speed, cattle give milk, hogs lay on fat—some, of course, to a greater degree than others—but they all exhibit the characteristics of their species and not the particular characteristics of other species. In other words, they inherit in the germ plasm all the potentialities of their species in greater or less degree, depending upon the strain to which they belong. In addition, the environment in which they develop and live determines how far these potentialities are developed. Therefore, if a horse is able to trot fast because of his having inherited the tendency and because the tendency has been given play for full development by a fast track, careful trainer, proper harness, etc., or if a cow inherited the tendency to produce large quantities of milk and this proclivity is subsequently fully developed by proper care, feeding, and management, is the assumption at all justified that these animals have acquired any new characteristics? The fair answer is that no new characteristics have been acquired by either the horse or the cow. Inherent characters have been developed, perhaps exceedingly well developed, but no new ones have been acquired.

The point at issue is whether or not any increased functional activity will be registered in the germ cells and thus influence future offspring. Under this heading Redfield's theory of "dynamic" evolution can be

discussed. This is the belief that the exercise of any organ or function results in a corresponding storage of energy in the germ cells, such that the effects are transmitted to the next generation—in other words, that these "acquired characters" are transmitted. This theory would postulate that, if a cow were developed from an 8,000-lb. two-year-old into a 16,000-lb. ten-year-old, the calf produced in her tenth year would be a much higher milk producer than the one produced when she was two years old, owing to the cumulative effect of the increased production she had attained, the same bull having been used to sire both heifers. This has a distinct practical bearing in all classes of livestock.

In his work to try to prove the existence of the inheritance of this acquired character or development in fast horses, Redfield first computed the average age of the immediate sires of the first 1,000 stallions taken alphabetically from the American Trotting Register, which he found to be 9.43 years. He then computed the average age of all the sires, four generations back, of the entire class of 2.10 trotters, a faster class than that dealt with previously, the upper limit for admission to the register being 2.30, and this average he found to be 13 years. From this material, he concluded that the 2.10 class was faster than the group first considered because their sires had gradually grown more speedy as they increased in age up to thirteen and that they had transmitted this dynamic development to their offspring.

Marshall critically points out the following shortcomings in Redfield's work. In the first place, he took in one case the immediate sire and, in the second case, all the sires included in the four-generation pedigrees. Marshall reminds us also that these four generations carry us back over the formative period of the trotting horse to the time of Hambletonian 10, who was himself a great sire of speed and left many sons and grandsons which, bred to faster mares, were even better sires of speed than he. Taking only the immediate sires of the 2.10 list, as was done with the first list of sires, Marshall finds the average to be 9.41 years, nearly the same figure Redfield secured for the first group, 9.43, and evidencing no advantage of the old sire over the young one.

In this matter of increased speed in succeeding generations of horses, it has not been proved that functional modifications have not been continued in the next generation, though it is a biased mind which would attribute all increase in speed to this factor and fail to recognize possibilities in amphimixis, possible mutations, better environmental influences, better harness and training methods, faster tracks, more skilled drivers, etc. Also, as has been suggested previously, is it not more likely that the germ cells caused the somatic changes rather than that the soma caused the germinal changes?

There is no conclusive scientific evidence in support of the inheritance of "acquired characters" regarding functional modifications or use and disuse of parts. This fact, however, should not influence breeders to decrease their efforts to provide the most favorable environment and to attain the fullest development of their breeding stock. Whether or not functional modifications are inherited, breeders should still seek the germ plasm carrying the greatest possibilities for high-class production and should seek, when offspring come from such germ plasm, to place it in the best environment and supply the best possible feeding and management in order that its inherent capabilities may be developed to the fullest extent. Not that one must believe that this acquired development will be transmitted, because there is no sure ground for any such belief, but it is desirable to know the horse of greatest speed, the cow of highest production, the meat animals with the greatest tendency to grow, and the sheep capable of the greatest production of high-quality wool and mutton, because, if in general "like does produce like," it is such germ plasm that should be used for increasing herds and flocks.

Pathological Modifications.—The fourth category, *viz.*, the inheritance of disease is also a consideration of vast practical importance. It should be borne in mind that, from a scientific standpoint, the only thing that is inherited is the germ plasm, more particularly, the various factors carried in the chromosomes. From this standpoint it will readily be seen that there is no more true inheritance in the case of disease than there was in the case of functional development. The problem, however, like the latter, has a very practical bearing, and although it may be said that in neither case has the affirmative been proved, yet this lack of proof does not necessarily preclude the possibility of its existence. One of the commonly cited cases under this heading is that of tuberculosis. This, however, is clearly a case of reinfection in the offspring, abundant opportunity for which is furnished in the intimate relations between parent and offspring, though it is very possible and no doubt true that the tendency or susceptibility to the disease is inherited in the defective germ plasm from which have come both parent and offspring. It is well known that it is possible to produce healthy calves from tubercular cows and bulls, provided the calves are at once removed upon being born and taken to a clean barn—in other words, that the opportunity for the parents to reinfect the offspring is removed.

In this regard, it may be well to mention the factor of immunity to certain diseases that exists in different species and varieties. If, for instance, a husky Irish policeman and an anemic Jew employed in a sweat shop were both exposed to the same kind and intensity of tuberculosis, the husky policeman would be more liable to succumb to the

disease, because, in the Jewish race, selection has established at least a partial immunity to this disease. The zebu is being crossed on the native cattle of Texas because of the former's relatively greater resistance to tick fever. The mulefoot hog is often claimed to be immune to cholera, though the claim has never been scientifically tested and substantiated.

The microscopic organisms causing various diseases, if present in the blood of a parent, may be carried to and deposited within the ovum before it is fertilized. Such organisms, although not part of the chromosomal material that alone is heritable, are carried in the same cell with it and will thus cause the disease to reappear in the offspring; in other words, the reinfection may come either previous or subsequent to birth. The organisms causing pebrine in silk moths, Texas fever in cattle, and syphilis in man are of this type, but, as Walter says, the disease is no more inherited than a grain of sand placed within the ovum would be inherited, though, of course, for all practical purposes, it amounts to the same thing, as the offspring will suffer from the disease in question.

A very interesting study of disease susceptibility and resistance has been reported by Dr. L. C. Strong of St. Stephens College. The following quotation[1] is taken from his paper:

> My first experiment dealt with the inoculation of a malignant tissue (adenocarcinoma) subcutaneously into a series of hybrid mice of known relationship. Two original stocks of mice were employed. Every individual of the first stock (*dBr*) grew the transplant progressively; and every individual of the second stock (albino) proved to be resistant to the same tissue. By crossing these two distinct races of mice, a hybrid generation, known as the first filial generation, was produced, all the individuals of which reacted to the transplant as did the first original stock, that is, all the individuals grew the transplant progressively. By mating two individuals of this hybrid first filial generation together, a second filial generation was obtained that contained two classes of individuals as far as their physiological reaction to the same transplanted tissue was concerned. Three individuals out of every four obtained were like the original susceptible race and grew the tumor progressively; one out of every four individuals was negative like the second original albino non-susceptible race; a typical 3:1 ratio was obtained. This experiment demonstrates, therefore, that susceptibility to a transplantable tumor is dependent upon the same ultimate mechanism that the inheritance of eye pigmentation apparently is dependent on. A particular individual grows a transplanted tumor because there is present in its ultimate make-up at least a single germinal determiner for a special physiological function that was obtained from the zygote that gave rise to the individual.

[1] STRONG, L. C., Inheritance of Cancer, *Jour. Hered.*, **15**(8):355–360, 1934.

Roberts and Card have reported[1] on a 10-year study of the inheritance of resistance to bacterial infection by *Salmonella pullorum* in chickens. Their summary and conclusions state:

From this experiment, ten years in duration and involving more than 29,000 birds, evidence has been obtained which clearly indicates that heredity is an important factor in resistance and susceptibility to infection with *Salmonella pullorum*. The existence of hereditary factors for resistance and susceptibility to pullorum disease is shown by the following results:

1. Selection was effective in producing strains of the domestic fowl more resistant than were unselected stocks in respect to infection by *Salmonella pullorum*.
2. The selected stocks were consistent in maintaining resistance through successive generations.
3. The F_1 generation produced by crossing resistant and susceptible stock was as resistant as the resistant parents.
4. Progeny of the F_1 individuals mated to resistant were significantly more resistant than were the progeny of the back-cross to susceptible.
5. In the F_2 generation susceptible and resistant strains were recovered by selection.
6. A susceptible male mated to susceptible females produced progeny which were much less resistant than were progeny of the same male mated to resistant females.
7. No significant difference was found between the progeny of susceptible and resistant females mated to the same resistant male.
8. Acquired immunity was not present in the experimental birds, the progeny of infected hens exhibiting no greater resistance to disease than the progeny of noninfected hens, infection and freedom from infection being determined by the agglutination test.
9. Resistance is dominant to susceptibility, but probably more than one gene is involved.
10. In an examination of the blood of noninoculated young chicks the number of erythrocytes was found to be greater in the resistant (6 out of 7 cases) than in the susceptible strain. The number of leucocytes was greater in the susceptible strain. The percentage of neutrophiles was lower in the resistant individuals (6 out of 7 cases). In inoculated chicks, the percentage of neutrophiles was much higher among the susceptibles at 6, 7, and 9 days than among inoculated resistant individuals of the same ages.

Psychological Modifications.—Many people believe in the ordinary principles of inheritance as far as physical traits are concerned but balk at applying these same principles to mental traits. On the other

[1] Roberts, E., and Card, L. E., Inheritance of Resistance to Bacterial Infection in Animals, *Ill. Agr. Expt. Sta. Bul.* 419, 1935. (Contains an excellent bibliography.)

hand, the belief that mental or artistic accomplishments are transmitted to one's offspring is particularly prevalent. True, if two parents develop artistic qualities their children are likely to be artistically inclined owing, however, to the fact that the parents had sets of genes which tended in this direction plus the very important additional fact that their children had a very favorable environment as far as the development of artistic qualities was concerned. Some experimental work with white rats (McDougall) has been interpreted as the inheritance of acquired learning of parent rats in choosing paths of escape after having been dropped into a tank of water. There appears to have been a more or less steady improvement in the succeeding generations of trained rats. In the fourteenth generation the best rat made 42 errors, the worst rat 102, with an average for all of 80. In the twenty-third generation the best rat made 3 errors, the worst 71, with an average of 25 errors for all. Even when reverse selection was practiced for two generations, improvement was evidenced. On its face, this looks like the inheritance of acquired learning. However, two important questions remain unanswered. Was the stock pure (homozygous) to start with? Was no selection, conscious or otherwise, practiced? Although the stock had been long inbred, McDougall states that there were "very large individual differences between the animals in respect of the rate at which they master their tasks."

Tryon has shown that the assortive mating of bright with bright and dull with dull rats can lead to the separation into bright and dull strains of rats as far as running a maze is concerned.[1]

Griffith's work indicating the transmission of acquired disequilibration in rats has not been substantiated, whereas Pavlov himself withdrew his earlier claims for the transmission of acquired learning through conditioned reflexes in mice.

There is as yet no clean-cut proof that acquired psychological modifications are inherited by the offspring. Because grammar schools have been in existence for several hundred years, one is tempted to ask, somewhat facetiously, why our present children do not enter high school or college rather than grammar school at the age of six, if the learning of their ancestors actually became part of the hereditary material.

Arguments against Inheritance of Acquired Characters.—The reasons for the general unwillingness to subscribe to the belief in the inheritance of acquired characters may be grouped as follows:

1. There is no known mechanism in the body capable of impressing soma or body changes on the germ cells.

[1] See Snyder, L. H., "The Principles of Heredity," pp. 395–398, D. C. Heath and Company, Boston, 1940.

2. The evidence, although partial in some cases, is by no means conclusive.

3. The theories of the continuity of the germ plasm and of germinal variation can account sufficiently well for all observed facts of heredity.

In order to study the effect of the soma on the germ cells, Dr. Castle at Harvard removed the ovaries of a white guinea pig and substituted the ovaries of a black guinea pig. The operation was entirely successful, and in due time the animal was bred to a white male and produced in all three litters totaling 6 individuals. This female was white (with substituted black ovaries) and was bred to a white male. Albino bred to albino in guinea pig invariably produces white offspring, but in this case all the offspring were black. Some of these in later breeding trials behaved as normal black guinea pigs would be expected to behave. This critical experiment shows that the ova produced by those two black ovaries which had been transferred to a white body were, after a year's location in their new environment, still producing black ova, and it is indeed inconceivable that they could ever have produced any other kind. This experiment indicates that there is no mechanism in the body capable of impressing soma or body changes on the germ cells, though it, of course, does not prove this to be absolutely so, it being impossible to prove a universal negative.

Summary of Inheritance of Acquired Characters.—Castle gives the following summary[1] on the inheritance of acquired characters:

The problem of acquired characters, after all, concerns only the higher animals. In the lower animals and in plants no such sharp distinction exists between body and germ-cells as we find in the higher animals. We may reproduce the entire plant from a cutting of root, stem, or even a leaf in some cases. Hence there is more chance in such cases of direct modification of the cells capable of reproduction, for most of the cells of the plant retain this capacity. In the lowest organisms (protozoa, bacteria) there is no distinction whatever between body and germ-cells. Every cell is capable of reproduction; and modifications produced in a cell by the environment are handed on directly to the next generation.

If in the lower organisms the potentialities of living substance can thus be altered, it seems reasonable to suppose that the same possibility may exist in the higher animals and plants, provided agencies capable of producing change are allowed to act on the germinal substance. It is the sheltered position of the germ-cells which seems ordinarily to exempt them from direct modification, but we cannot safely assume that they are in all cases free from such modification. Experiments of Stockard show that in guinea-pigs repeatedly intoxicated with alcohol, the germ-cells are enfeebled so that offspring of such parents, whether

[1] Castle, W. E., "Genetics and Eugenics," pp. 87–90, Harvard University Press, Cambridge, Mass., 1930. (Reprinted by permission of the President and Fellows of Harvard College.)

male or female, are more likely to be feeble and sickly, and so to die. Experiments of Hertwig show that similarly the germ-cells of frogs are capable of being injured by emanations of radium in consequence of which enfeebled or abnormal offspring may be produced.

Guyer and Smith have produced probably the best existing evidence for the artificial production of heritable defects. Injecting into the bodies of fowls the pulped lenses of rabbit eyes, they induced the production in the fowls' blood of antibodies which would neutralize harmful effects of the foreign material. Blood serum was then obtained from these immunized fowls and this serum was injected into the circulation of pregnant rabbits and made its way, it is thought, through the placenta into the circulation of the developing fetuses, where it interfered with the proper development of the eye in a certain number of embryos. Eye-defects such as opaque lenses, under-sized eyes, and eyes rotated out of their proper position, were thus obtained in two different and unrelated races of rabbits. These defects reappeared sporadically among the inbred descendants of the abnormal rabbits, and so may be regarded as having become hereditary. Guyer and Smith consider the mode of inheritance that of a recessive Mendelian character, though fewer recessives are reported than theory demands; but this may be explained as due to the authors' failure to detect cases of slightly defective eyes, or to the failure of the character to find somatic expression in all cases.

In a third unrelated series of animals, Guyer and Smith injected pulped rabbit lens directly into the circulation of pregnant rabbits, and in this case also they obtained from one treated mother one young with defective eyes in a litter otherwise normal. The defect was transmitted in this case also.

The eye-defects in the experimental rabbits of Guyer and Smith were transmitted through male as well as through female parents. The authors believe that the antibodies artificially produced by the injected foreign bodies affected the constitution of germinal determiners at the same time that they affected corresponding somatic structures in the same individuals. In other words they favor "parallel induction" as an explanation of their results.

Finlay (1924) has repeated on mice the experiments of Guyer and Smith on rabbits, but with wholly negative results. He used rat lens, sheep lens, and ox lens to produce antibodies in pregnant mice, but without observing any eye-defects in the young of either the F_1 or the F_2 generations.

On the other hand, Little and Bagg, by X-raying pregnant mice, obtained young with pronounced eye-defects which were apparently inherited in the next generation as recessive characters. Hansen, too, X-rayed rats in utero and obtained eye and other defects but without studying their inheritance. Stockard had previously obtained similar eye-defects in guinea-pigs by exposing the mothers to alcohol fumes. Hansen and Stockard are agreed that a variety of harmful agencies acting during the embryonic development of a vertebrate may so interfere with the complicated process of development of the eye as to lead to defective end results. They regard the defective eyes of the rabbits of Guyer and Smith not as specific effects of lens antibodies, as those authors supposed, but as due to disturbed development, maintaining that like results can be produced by any other disturbing agency.

If the germ-cells are capable either directly or indirectly of modification by outside agencies, evolution guided by the environment must be in some measure at least a reality. The truth then lies neither in the extreme Lamarckian view that all acquired characters are inherited nor in the extreme Weismannian view, that no extraneous influences modify the germ-plasm, but somewhere in between.

Practical Phase of Inheritance of Acquired Characters.—Breeders should continue to develop their animals to the utmost. If this development is cumulative from generation to generation, breeders will profit thereby. If not, they will at least be able to see which animals are inherently capable of responding in the fullest degree to a favorable environment, and then, through selection of these animals as breeding stock and through wise matings, they will be able to bring about a gradual improvement in the stock under their care.

Telegony.—Telegony may be illustrated by the more or less common belief that, after a female has borne young by a certain male, her subsequent offspring will show characteristics derived from the previous sire. The classic example is that of a mare which bore offspring by a quagga and later produced horse colts that showed some striping. Numerous attempts have been made to confirm this by crossing mares and zebras, but in all cases they have failed. The basic elements that determine the characters of any individual are the ovum and the spermatozoon uniting to produce it. Spermatozoa from this first service could not possibly live over a gestation period in the female organs of any higher species to fertilize the next egg, as they live for a very few days at the most. If this first offspring had any influence on other undeveloped eggs in the ovaries, it would come under the heading of the inheritance of acquired characters, for which there is no conclusive proof. Mumford and Hutchinson made investigations in the mule-breeding district of Missouri, where mares often bear mule and later horse colts, but could find nothing to substantiate telegony. In the light of present knowledge of inheritance, telegony has neither experimental nor theoretical basis.

Maternal Impressions.—Belief in maternal impressions assumes that what a pregnant mother may see, hear, or experience may influence her offspring. In general, this old belief can be repudiated also, because, as Marshall points out, if it worked, all calves born in the spring up north would tend to be white because the mothers have viewed a white landscape all winter, and, similarly, calves born in the fall would be green. There is no direct nerve connection between parent and offspring to afford means for transporting ideas. Animal experiments have all given negative results in this field. It is, indeed, a fortunate provision of nature that in the higher animals the embryo is so well protected from all external influences. If maternal impressions were actually registered

on the offspring, all types and races would have long ago become a hideous, conglomerate mess.

Atavism or Reversion.—These terms, meaning the reappearance of some ancestral trait or character after a skip of one or several generations, are often encountered in the older literature on animal breeding. Such reappearances were more or less mysterious before the physical basis of inheritance was understood. The birth of a red Angus when the past four generations have been black is known to be due to each parent supplying a gene for red. Recessives may be carried along, hidden by dominants, for any number of generations. Whenever two recessives come together, or, in other words, whenever the dominant gene is lacking, the "atavistic" character will be evident. Atavism or reversion is the sudden reappearance of some ancestral trait, but there is nothing mysterious about it, for it is one of the normal manifestations of the hereditary mechanism.

Summary.—We have tried to indicate in this chapter that the environment does play a large part in variation. Any organism inherits a certain "norm" based upon the nature of the genetic content of egg and sperm that unite to produce it. This "norm" however, may be influenced by many internal or external factors. It is like any elastic material, dough or newly mixed concrete. Within limits it can be molded into different forms by the environment. However susceptible the somatic tissue may be to molding, there is no conclusive evidence that molding of the soma itself can have any influence on the germ cells. By regulating food intake, any parent could be one-third lighter or heavier in weight, but his children's actual weight would not thereby be directly influenced. If we want heavier children, we will naturally select as the parents those who most readily put on weight. Variation therefore can be a very useful tool in directing selection. The task of differentiating between environmental and hereditary variation and between the various types of the latter is not easy but on its accomplishment depends the breeder's ultimate success. Variation can indicate new and desirable gene combinations. Seeing, seizing, perpetuating, and amplifying these lie at the base of any breeder's progress.

References[1]

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[1] See lists at end of Chaps. XI and XII.

CHAPTER XVII

SEX DETERMINATION

Sex in the higher animals is a relative matter in all except one respect, *viz.*, the kinds of cells produced. And even in this respect the different types of cells, ova and spermatozoa, are essentially alike regarding chromosome content and differ only regarding cytoplasm and motility. For obvious reasons, man has always been keenly interested in the factors determining sex, with the hope that he might ultimately find ways and means of controlling them to his own benefit. Because of the wide interest and enormous value of such knowledge, there have been conceived in men's minds a great number of hypotheses regarding sex determination and its control. It is said that over 500 of these theories have been recorded. One theory states that the right testicle produces male-producing spermatozoa and the left testicle female-producing spermatozoa. The same idea is often applied to the ovaries of the female. Many breeders believe that alternate heat periods are productive of opposite sexes. The same idea is sometimes applied to service at early and late portions of the heat period. Such theories as these have easily been proved false. One of the most weird superstitions states that "if a man has a sty on his eye, he concludes his aunt is pregnant. If the sty is on the upper eyelid the offspring will be a boy; on the lower a girl." Any theory for sex determination must, from the very nature of the case, be correct half the time, the offspring, of necessity, being either male or female, in most species these occurring in equal numbers.

Sex Ratios.—In most of the higher species the two sexes are born in approximately equal numbers, whereas in some of the lower species there are great differences in numbers of the two sexes. Since in some of the multiparous species many embryos die and are absorbed during gestation, the actual number born is neither a correct record of fecundity nor is the sex ratio at birth necessarily the same as at fertilization if there is a differential survival rate between the sexes. Both Hammond and Parkes have shown that in swine there is a preponderance of males soon after fertilization, but in this species the males are more liable to die during embryonic development, so that at time of birth they exist in approximately equal numbers, and Parkes has reported the same phenomenon in mice. Other evidence indicates that in mammals,

generally, there is a heavier fetal death toll on the male than on the female embryos. For these reasons the sex ratio at fertilization is sometimes referred to as the *primary* sex ratio, that at birth as the *secondary*. In this discussion, sex ratio means that existing at birth.

Sex ratios are expressed as the number of males per 100 females or as the percentage of males of the whole number born. For statistical reasons the latter figure is preferred.

Table 26 gives some sex ratios that have been found in some of the higher animals.

TABLE 26.—SEX RATIOS IN FARM MAMMALS AND MAN*

Animal	Number of births studied	Percentage of males in all births	Number of studies
Horse	1,249,337	48.9–49.9	6
Mule	1,416	44.3	1
Cattle	155,579	49.4–51.5	3
Sheep	91,640	49.5	1
Swine	74,639	50.6–52.3	3
Goat	3,000	50.1	1
Man	....	50.7–51.7	Several

* Adapted from LUSH, J. L., "Animal Breeding Plans," p. 315, Collegiate Press, Inc., of Iowa State College, Ames, Iowa, 1937. (By permission of author and publisher.)

If sex is determined by the chromosomes and genes, as seems most probable, and the heterogametic spermatozoa (in mammals) are produced in approximately equal numbers, then differences in fertilization rate must be due to differential activity of the two types of spermatozoa or to differential selectivity by the ova. If there is a differential fertilizing rate between the male- and female-conditioning sperm but approximately equal numbers of the sexes at birth, then there must also be a differential mortality rate between the two types of embryos, with the male embryo in mammals apparently having a higher rate of mortality.

Chromosomes and Sex Determination.—*Drosophila melanogaster*, the common fruit fly, has been more thoroughly studied, from the standpoint of inheritance, than any other species, and the study has yielded a rich harvest. Along with the knowledge gained regarding behavior of genes and chromosomes in transmission from parent to offspring has come definite knowledge regarding sex and what determines it. There are two sources of such information, one cytological and the other the behavior of sex-linked factors. Cytology has established the fact that the normal number of pairs of chromosomes in *D. melanogaster* is four. Of these, three pairs are autosomes and one pair sex chromosomes, and although

both sexes have autosomes that are morphologically identical, there is a characteristic difference between male and female regarding the sex chromosomes. The female has two so-called X chromosomes, whereas the male has one X chromosome and one Y chromosome. Figure 127 should make this clear.

After reduction has taken place, as shown in the diagram, there can be but one sort of ovum produced; *i.e.*, every ovum will contain one member of each pair of chromosomes, and each one will, therefore, contain one X chromosome. In the male, after reduction, there will be two kinds of spermatozoa, both of which are similar as to autosomes but different as to sex chromosomes, one having an X chromosome and

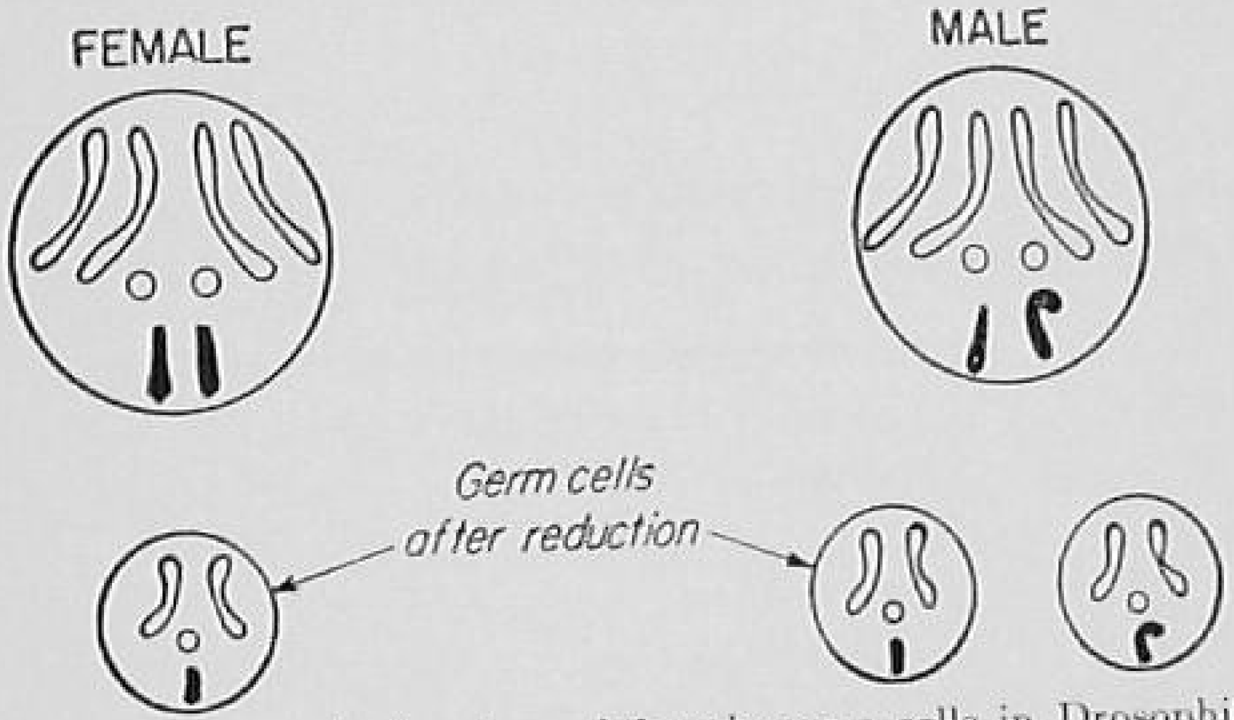

FIG. 127.—Diagram of nuclei of male and female germ cells in Drosophila, showing the kind of ova and kinds of spermatozoa produced.

the other a Y chromosome. Presumably, these kinds of spermatozoa
are produced in equal numbers. Starting with an ovum containing an
X chromosome and adding a spermatozoon also containing an X chro-
mosome will give an individual with two X chromosomes, or a female.
Starting with an ovum containing an X chromosome and adding a
spermatozoon containing a Y chromosome will give an individual con-
taining both an X and a Y chromosome, or a male. Cytological evidence,
therefore, proves beyond a reasonable doubt that, in Drosophila, sex
is determined at time of fertilization by the kind of spermatozoon that
fertilizes the ovum, for the sexes invariably show the differences just
outlined.

Nondisjunction in Drosophila.—An aberrant type of reduction in
Drosophila, occurring very rarely, lends support to the chromosomal
interpretation of sex determination. This is the feature of nondis-
junction, which has been worked out by Bridges. This investigator
has shown that occasionally reduction in the germ cells takes place in
such a way that after synapsis the two sex chromosomes of a female
do not disjoin but both of them pass to one pole of the cell, giving rise

to egg cells of the constitution XX and O instead of two normal egg cells, each containing one X chromosome. The relations holding may be made more clear by means of introducing a sex-linked character. If, for instance, a white-eyed female ($rXrX$) is mated to a red-eyed male (RXY), all the normal daughters will be red-eyed and the normal males white-eyed.

Sperms	Eggs	
	rX	rX
RX	$RX\ rX$	$RX\ rX$
Y	rX Y	rX Y

If, however, in a white-eyed female, nondisjunction occurs, individuals of the four types indicated in the diagram below should be produced.

Sperms	Eggs	
	$rX\ rX$	O
RX	$RX\ rX\ rX$	RX O
Y	$rX\ rX$ Y	Y O

As a matter of fact, the $RXrXrX$ individuals usually die, as do also the YO individuals, the former, as Morgan suggests, because of too many X's and the latter presumably because they lack an X chromosome. In other words, if the genetic constitution is thrown too far out of balance, the animal cannot survive. The other two individuals $rXrXY$, a white-eyed daughter, and RXO, a red-eyed male, are the exceptions to the normal expectancy.

Breeding results from such individuals in F_2 (which the student can diagram) give results that would be expected from individuals of such chromosomal make-up, and the point to be stressed here is that, in either F_1 or F_2 individuals, two X chromosomes result in producing a female and one X chromosome a male.[1]

These results not only furnish very strong proof of the chromosome theory of sex, but serve also to show how a knowledge of the actual mechanism involved leads to the discovery of how a change in the mechanism gives a new output.

[1] Morgan, T. H., "The Physical Basis of Heredity," p. 203, J. B. Lippincott Company, Philadelphia, 1919.

The conclusion that females behaving in this manner must contain a Y chromosome was confirmed by the cytological demonstration that showed in them two X's and a Y.

The distinguishing feature of the XY type of sex inheritance, which prevails in mammals, is that the female is homogametic and the male heterogametic for the sex chromosome. It was thought at one time that the Y chromosome was simply a neutral and more or less useless mate for the X chromosome. This, however, has been disproved. Only one dominant gene has been demonstrated in the Y chromosome of Drosophila, but the fact that all males of the genetic constitution XO, *i.e.*, lacking a Y chromosome, are sterile leads one to the conclusion that something in the Y chromosome is essential for fertility—in other words, for normal maleness. It is known that in some species certain characteristics are passed along always and only from father to son, indicating that their determiners must be in the Y chromosome.

The Theory of Genic Balance.—In several species of animals, there have been found individuals that partook partly of the characteristics of both sexes, *i.e.*, were in fact partly male and partly female. This was difficult to explain on the basis cited above: that one X results in producing a male and two X's a female. Goldschmidt first studied these so-called "intersexes" in the gypsy moth *Lymantria dispar*. He found that in the F_2 of a cross between Japanese males and European females half the daughters were intersexes. Goldschmidt after an extended genetic study concluded that sex was due to a balance between male- and female-producing genes in the sex chromosomes.[1]

These and other crosses leave no doubt that the tendency to form intersexes is inherited in a regular manner. In moths, in general, the males are XX, the females XY; and within pure races this sex chromosome constitution is decisive. In crosses between races which produce intersexes, however, two further variables have to be taken into account; one is a factor for maleness in the sex chromosome which has different strengths, that is, presumably occurs in different allelic forms in different races; the other is an influence tending in the opposite direction toward femaleness; also varying in different races, and this seems to be inherited through the cytoplasm of the eggs, that is, all the eggs of an individual are alike with respect to the strength of this tendency. The sexual condition of the offspring of crosses is decided by the relative strengths or balance existing between these two opposed tendencies. This interpretation is supported by extensive evidence from many interracial crosses.

Goldschmidt and his coworkers have also proposed a mechanism by which these sex genes influence the development of the sexual characters. The essential

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," 3d ed., p. 261, McGraw-Hill Book Company, Inc., New York, 1939.

assumptions here, as found first in the worm Bonellia, established by a careful study of the embryological development of Lymantria and later extended to Drosophila, are that intersexes in these forms begin their development as males (or females) and develop as such up to a certain critical point, the so-called "turning point," after which their development is of the opposite sexual type. The mixture of male and female parts is thus explained as due to the supersession of one type of sex tendency by the other. Sex development is conceived as essentially a competition between opposed tendencies in which the race is eventually won by that type of process (either male or female) which proceeds most rapidly at the critical period of determination of each organ or part involved.

The discovery of certain individuals in Drosophila cultures, which in their sex characteristics were between (intersexes) or beyond (supersexes) the normal male or female limits, has yielded further evidence that sex manifestations are due to a certain balance between the genetic content of the automosomes and that of the sex chromosomes. Bridges has shown that the normal balance between two sets of autosomes (2*A*) and two sex chromosomes (2X) produces a female, and the balance between 2*A* and 1X produces a male. That is to say, the autosomes have genes tending to produce maleness, which they do when working in conjunction with the genes found in one X chromosome. When, however, there are 2X chromosomes present working in conjunction with 2*A*, the result is a female; *i.e.*, the genes in the X chromosomes are preponderately female-producing. A graded series of sexes have been found or produced experimentally as indicated in Table 27.

TABLE 27.—RELATION OF SEX TO CHROMOSOMES IN *Drosophila melanogaster*

Sex type	Formula	X = 100	*A* = 80	Sex index
Superfemale	2*N* . . . 3X:2*A*	300	160	1.88
	4*N* . . . 4X:4*A*	400	320	1.25
Female	3*N* . . . 3X:3*A*	300	240	1.25
	2*N* . . . 2X:2*A*	200	160	1.25
	1*N* . . . 1X:1*A*	100	80	1.25
Intersex	4*N* . . . 3X:4*A*	300	320	0.94
	3*N* . . . 2X:3*A*	200	240	0.83
Male	2*N* . . . 1X:2*A*	100	160	0.63
	4*N* . . . 2X:4*A*	200	320	0.63
Supermale	3*N* . . . 1X:3*A*	100	240	0.42

It will be seen from this table that a normal balance between autosomes and sex chromosomes 3*A* and 3X or 2*A* and 2X results in a female, whereas a preponderance of the X ingredient results in a superfemale

and a preponderance of the autosomal ingredient results in varying degrees of manifestations of maleness.[1]

If we represent the net effectiveness of the female tendency genes in the X by 100, then we should represent the net male effectiveness of a set of autosomes by some lower number, approximately 80. In the 2X2*A* individual the ratio of female effectiveness to male effectiveness is 200:160, or 1.25:1. On this formulation an index of 1.25 corresponds to a normal female. As is indicated in Table 27, this same index of 1.25 holds for 3*N* individuals, for the ratio is 300:240, or 1.25:1. The identity of sex indices for the 3*N* and 2*N* forms corresponds to the observation

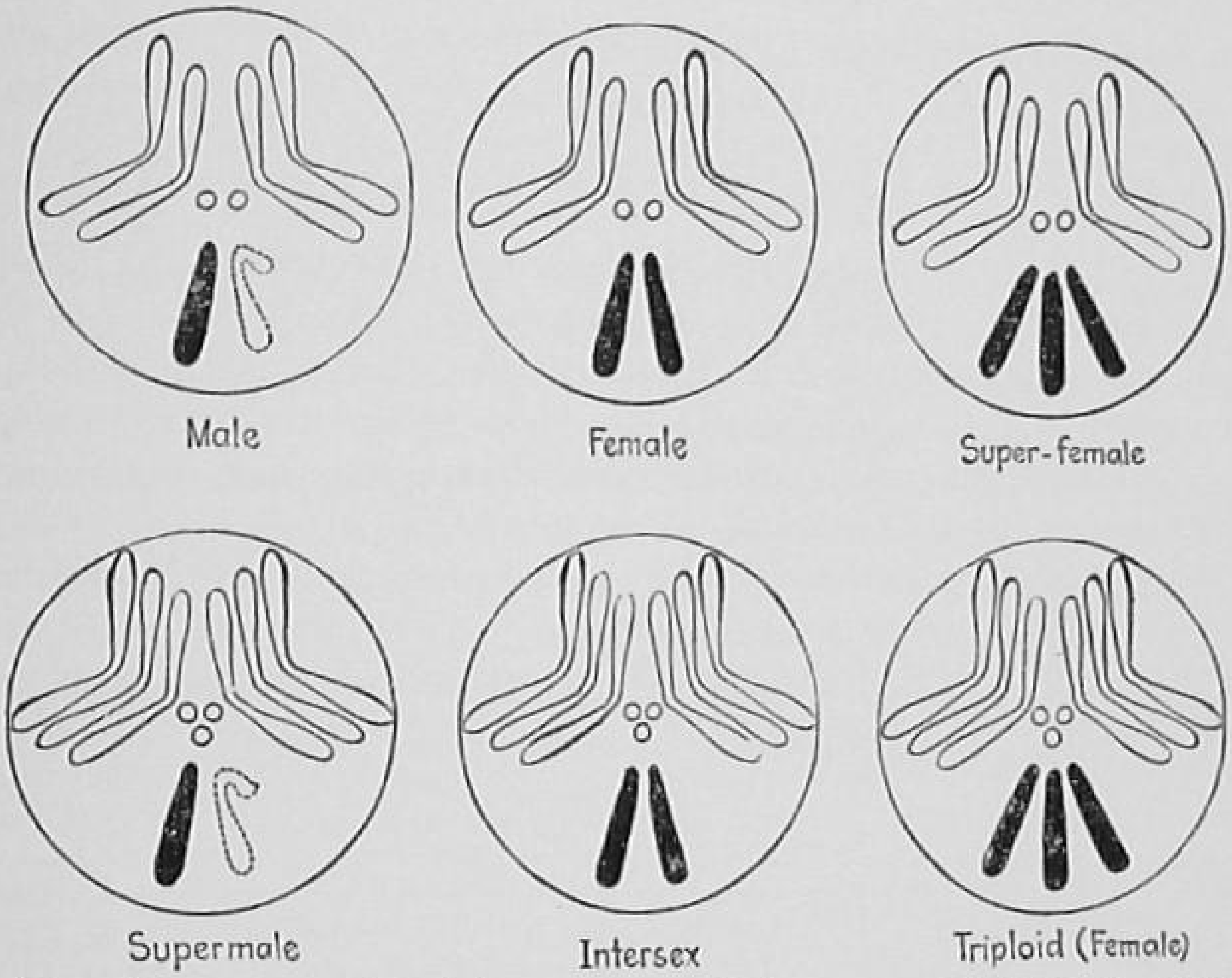

Fig. 128.—Effect on sex of the balance between X chromosomes (solid) and autosomes (outlined) in Drosophila. (*Rearranged from Sinnott and Dunn, Principles of Genetics.*)

that there seems to be no sexual difference between them. In the X2*A* individual the ratio is 100:160, or the sex-index is 0.63, that of the standard male. The sex-index of the 2X3*A* intersex is 0.83, intermediate between the 1.25 of femaleness and the 0.63 of maleness.

New tests of the general validity of the genic balance formulations as a ratio between opposed sets of genes came from several sources. First, both myself [Bridges, 1925] and L. V. Morgan found tetraploid individuals. We observed that these 4X4A individuals were completely normal and fertile females, practically indistinguishable somatically from 3*N* females. That the sex was not

[1] Allen, E., Danforth, C. H., and Doisy, E. A., "Sex and Internal Secretions," 2d ed., pp. 40–42, The Williams & Wilkins Company, Baltimore, 1939. (Paper by C. B. Bridges.)

changed when the chromosomes were doubled is in the best conformity with the ratio formulation and is difficult to account for on the arithmetical system (Schrader and Sturtevant 1923).

A second and more striking test came from the work with the haploid or one N individual in Drosophila. It was predicted that this type should be female in sex since it must have the same ratio of X to A as the $2N$, $3N$, and $4N$ females. No such haploids were then known for Drosophila, and this expectation of femaleness was in direct opposition to the fact that all of the many haploid animals known up to that time were males without exception. By a special technique a few mosaic individuals, one in several thousands of normals, were found in a special strain of flies. These rare mosaics have parts of their bodies haploid as shown by autosomal genes and by the smaller cell size. In some of these mosaics the haploid regions included body parts which enabled the sex to be diagnosed. They were actually female as expected (Bridges 1925). Since then at least three other workers have found Drosophila mosaics in which haploidy and femaleness seem to be associated.

In unpublished results Sturtevant has found that the 2X4A is a male and that 3X4A individuals are intersexes, both fitting into place in the series.

The observation of $1N$ = ♀ in Drosophila no longer stands alone. Frankhauser (1937) secured haploid embryos of the newt, one of which lived nearly through metamorphosis and showed definite female-type gonads, conforming to expectation from the 2X2A formula for the normal female.

In applying the concept of genic balance to sex Bridges (1922) had made the postulate that female producers predominate in the X and are scattered throughout it at random in the same sense as are the producers of eye color or any other character. Experimental proof of these assumptions were obtained by Dobzhansky and Schultz (1934) through the use of fragments of X (duplications) of various lengths and taken from various regions of the X, and also by deficiencies or losses of sections of the X.

For a sensitive test of the sex effect of these extra pieces or losses of sections of X the grade of the intersexes was used, marked off into six classes from extreme male-like to extreme female-like types. Thus, a $3N$ female all of whose X's carried the recessive yellow was crossed to a male whose X was also yellow, but which was hyperploid for a non-yellow fragment extending from the left end of the map to beyond the locus prune. Half the intersexes would be without this duplication and would be yellow while the other half would carry it and would have the yellow "covered" by the wild-type allel in the fragment.

The experimental findings were that each of the dozen duplications tried causes a shift in the female direction, none in the male direction, as compared with the siblings without it. Moreover, the longer the piece of X used the greater was the shift toward femaleness—even resulting in intersexes fertile as females! On the other hand, one deficiency shifted the intersexes toward maleness, while another, involving mostly the "inert" region at bobbed, was neutral in effect. Since these duplications covered all of the X chromosome, the conclusion follows that no part except the "inert" region is free of female producers in excess of male producers.

Sex-producers and Sex-differentiators.—From the numerous examples of mutant sex-characters in Drosophila, Zea, and other forms, it is clear that a fairly large proportion of the genes must be concerned with the production of the normal sex organs in their normal grade of development. All these genes whose action is part of the normal sex-development, which would have another outcome if mutant alleles were present instead of these normal genes, one may call "sex-producers." This includes the so-called "sex-modifiers," where the degree of effect is perhaps less than some of the other genes or the effect is observable only or predominantly in one or the other sex.

Any of the above producers of sex may become a "differentiator" of sex in mutant form as contrasted to the standard form in the same cross. Some may require special circumstances such as the sensitive condition in 2X3*A* intersexes or the cooperation of other genes to bring out their differential action. Some allelomorphic differences are so slight in effectiveness as only to change the individual from female to male or from male to female as shown in fishes, maize, and Habrobracon.

The difference between a producer and differentiator of sex may be illustrated by an analogy. As equal weights are added to the pan of a balance the beam finally tips. Let us say ten weights left it untipped and after the eleventh was added it tipped. But this eleventh weight has no more intrinsic significance in the tipping than each of the weights added before. If any one of them had been omitted the beam would not have tipped when this one was added. All together produce the result. The last one is the differentiator of the position of the beam.

Genes and Sex Determination.—We have seen that sex is not determined by any specific whole chromosome, but rather that it appears to be due to certain balances between genes located in both the autosomes and the sex chromosomes. Recent work by Patterson and his students at the University of Texas has seemed to indicate the localization of the genes in the X chromosomes, which must be present in duplicate to produce a female or in a single dose to produce a male. This was accomplished by treating flies with X rays, with the result that the X chromosome was broken into various-sized fragments. Thus, stocks of flies could be made up containing one normal whole X chromosome and various-sized fragments of another X chromosome. This procedure indicated that a certain small region of the X chromosome between the genes for pleated and garnet was the essential portion operative in throwing the balance of all the genes toward the male or the female side. This is shown diagrammatically in Fig. 129.

It thus appears that the genes or gene in the X chromosome which reacts with autosomal genes in determining sex are located in this small region of the X chromosome.[1]

[1] *Ibid.*, pp. 25–28.

Sex-mosaics and Gynandromorphs.—An interesting and important phase of sex-determination is involved in the production of mosaic individuals which are of both sexes at once, but in different body-regions, and with a sharp line of demarkation which at the same time corresponds to a difference in genetic or chromosomal constitution. A comprehensive survey of gynandromorphs in all types of animals has been given by Morgan and Bridges (1919) and a special review of the Drosophila cases by L. V. Morgan (1929).

Doncaster (1914) in studying sections of fertilized eggs of the moth Abraxas observed an occasional egg with two separate maturation spindles and two female pronuclei each about to be fertilized by a separate sperm. He suggested that these pronuclei could differ as to whether they carried a sex-chromosome or not (female heterogametic) and consequently the double fertilization process could give rise to gynandromorphs. Definite proof of the occurrence of such dizygotic gynandromorphs came in Drosophila with the discovery of sex-mosaics which were at the same time mosaics for autosomal marker characters. Occasionally

FIG. 129.—Diagram of section of X chromosome determining sex. (*After Paterson.*)

such dizygotics were mosaics for autosomal characters in two different autosomes, though it is rare to make a cross that would show this. The first of the clear dizygotic gynandromorphs was one found by Bridges (Morgan, Bridges, and Sturtevant, 1925) in a backcross involving two second-chromosome recessives, vestigial and speck. The right side of the body was mostly female and showed speck; the left side was mostly male and showed vestigial. The explanation is that the right side had come from an X-egg carrying speck, fertilized by an X-sperm carrying vestigial and speck. The left side came from an X-egg carrying vestigial, fertilized by a Y-sperm carrying vestigial and speck. Some 20 dizygotic mosaics have been found in Drosophila, though the majority were alike in sex on the two sides.

In Drosophila there is another type of gynandromorph, of which several hundred have been found. These start as XX zygotes and give rise to XO male tissues on one side or part of the body. The male tissue results from the loss or "elimination" of one of the two original X chromosomes, the autosomes all remaining diploid. If the elimination takes place at the first cleavage, half of the body becomes male; if at the second, only about a quarter.

A striking example of such bilateral gynandromorph was one found by A. M. Brown and included in the general account of gynandromorphs by Morgan and Bridges (1919). This gynandromorph occurred in a cross between an eosin miniature male and a female heterozygous for eosin and miniature. The male right side showed miniature and eosin, while the left side was female and wild-

type. Presumably the gynandromorph started from an eosin miniature/wild zygote and at the first cleavage division one of the daughter chromosomes of the maternal wild-type X chromosome lagged upon the spindle and was lost. Hence one cell retained the original constitution and developed as female while the other was XO in constitution and developed as eosin miniature male.

In case the male parts of an elimination gynandromorph include the abdomen, such an individual can be mated as a male. But he is invariably sterile, as he should be from the XO constitution of the male parts.

That an X-chromosome only, and not the autosomes, is involved in the elimination was shown by a test proposed by Muller, namely that a cross be made involving the sex-linked characters yellow and white, as markers for the X, and ebony or some other recessive as a marker for the autosomes. Gynandromorphs in such crosses showed sex-linked characters in the male parts but never the autosomal ones—except those due to double fertilization, as noted above.

Morgan and Bridges (1919) studied carefully about 100 gynandromorphs and found that the maternal X was eliminated about as frequently as the paternal X. In experiments in which all flies were counted 40 gynandromorphs occurred in 88,000 flies, or 1 in 2,200. The line of separation was usually sharp with respect to both sex and whatever sex-linked characters showed in the different areas. Of the dozens of sex-linked characters seen in the gynandromorphs all were autonomous in development locally except vermilion, and, to a slight extent Bar (Sturtevant 1920).

A third type of sex-mosaic was found by Bridges (1925) in crosses in which the mother was heterozygous for the sex-linked dominant Minute-*n* and the father showed one or more sex-linked recessives, such as yellow, eosin and singed. The Minute-*n* daughters frequently (10 to 40 per cent) showed one or more spots that were not Minute, but were yellow eosin and singed. Some of these spots could be classified as male by including eosin (lighter in ♂) or the fore-leg with its sex comb. The explanation offered by Bridges was that Minute-*n* induced frequent elimination of the *Mn*-bearing X in the somatic calls. This occurred relatively late in imaginal disc development, thus accounting for the small size of the spots. But Stern (1936) has studied their origin thoroughly and shows that they are due to crossing-over in the imaginal cells. This crossing-over leads automatically to somatic segregation, since the equational separation of spindle-attachments draws the crossover terminal regions into separate cells. Stern finds that the homozygous *Mn* spots then die, leaving the homozygous *y sn* spots which were observed by Bridges. Stern finds that most spots are XX and female. Male spots, such as those detected by Bridges, do occur, principally when the *Mn* mother carries an extra Y chromosome. Then somatic segregation gives XY male spots, instead of XO spots as Bridges supposed.

Endocrine Function in Sex Differentiation.—In the earliest forms of life, there probably were no distinct sexes. These organisms reproduced only by fission, or budding, where the division of the parent was very unequal. This, of necessity, meant that the offspring would be very simi-

lar to their parents, for a considerable portion of the parent went to form each new offspring, although an occasional mutation might happen. Eventually the division of labor among the cells making up organisms meant that certain cells were developed for the particular purpose of reproduction. At length, there apparently came to be formed different types of reproductive cells, which had to unite to produce a new organism. At first these cells were produced by one parent (hermaphrodite), but eventually there came a time when the union of dissimilar cells, particularly as far as cytoplasm is concerned, produced by two separate individuals was necessary to form the beginning of a new individual, and finally the two sexes themselves came to be quite different, in part because of the constitution that allowed one to produce eggs and the other spermatozoa. Sexuality has therefore come about through a long line of evolutionary development, and the advent of unisexuality probably greatly speeded up the evolutionary process because of the gene differences brought together in the new organism, and the fact that the new organism in turn was destined to give a random, sample half of its diversely acquired genetic material to each of its offspring.

Many plants and animals are still of one sex in one portion of the body and the other sex in another portion. In some the production of male or female gametes alternates or varies in time owing probably to environmental influences. In higher mammals, of course, the two sexes are recognizably different both in regard to their sexual products (eggs and spermatozoa) and their somatic differentiation. These differences are basically genetic, *i.e.*, owing to differences in gene complements, but superimposed on the genic differences are those lately discovered to be of an endocrine nature.

It is probable that in Drosophila and many other species of lower animals the same mechanism, *i.e.*, the genes, underlies both these phenomena. If, at the first cell division in a female Drosophila zygote, one of the resulting daughter cells gets only one X chromosome, a gynandromorph half male and half female results. If the discrepancy occurs at the second cell division, approximately one-quarter of the resulting organism will show male characteristics.

In the higher vertebrates, however, the evidence indicates that, although the genic balance usually determines the sex of the individual, this is subject to another, hormonal, control. Lillie has shown that the freemartin (abnormal sexual female) in cattle arises where the choria of unlike sexed twins become fused and the blood vessels anastomosed so that the blood of the two embryos becomes interchangeable. Lillie has shown that this is due to the influence of a hormone secreted by the male gonad which, when carried by the blood into the female calf,

replaces the development of normal ovaries and, to some extent, the female accessory organs of reproduction with testes and male ducts. The female is genetically a female and appears phenotypically as a female, but the male sex hormone in its blood during early embryonic life prevents the development of a normal set of female genital organs and substitutes an imperfect male set. Hughes has reported the same phenomenon in the pig. Specifically, the medullary portion of the gonad forms sex cords instead of the normal medullary cords of an ovary.

Experimentally, this has been accomplished in several of the lower animals by surgically joining embryos, by gonad transplantations, and by the injection of sex hormones into embryos. The female sex hormone injected into an embryonic genetic male chick causes the left testis to become a flattened, ovarylike, ovotestis, and the right testis is sometimes affected and the oviducts persistent. Injection of the male sex hormone into an embryonic, genetic female causes the cortex of the left ovary to thin out and the medulla to hypertrophy and transform into testicular tissue at the hilus.

The first set of sex cords that pass into the gonad form the medulla, and this later forms the sex cords of the male. The medulla is present in the ovary, and later there is added the cortex. The ovary, therefore, consists of two tissues of different physiological capacities. In the early stages, the male gonad also has a cortex, but this does not persist. The seminal cords of the medulla are already established at the time of morphological sexual differentiation, and the male gonad, therefore, starts to function as an endocrine gland before the female gonad to which the cortical layer is added somewhat later.

Whether male or female sex organs begin to develop in the early embryonic stages is conditioned by the chromosomal make-up. There is apparently no real sex differentiation, however, until after the primordial sex tissue has been laid down in the embryo. The male organs of reproduction have their homologues (similarity of origin, not function) in the female and vice versa (penis and clitoris or uterus and uterus masculinus, etc.); in other words, the primordia for both sexes are present, the make-up of the chromosomes being the determining factor as to which will begin to develop, the full development in turn being conditioned by hormones secreted by testicles and ovaries.

Sex is, therefore, determined by the genic balance, and actual differentiation is brought about by the sex hormones. That the chromosomes or genes are not of themselves able to bring about sex differentiation in the higher animals is well illustrated by the results following castration (or spaying). If castration of mammals is performed soon after birth,

the two differently sex-determined classes, male and female, tend to remain the same; *i.e.*, sex differentiation does not ensue. The castrates have the sex genes XX or XY in all the cells of their bodies, but male or female secondary sex characters do not develop in the absence of the gonad hormones (see Chaps. IV and V).

Sex Reversal.—Sex reversal has been produced experimentally in several lower forms of animals. In the toad, for instance, there is a rudimentary organ, composed of rounded cells that resemble egg cells, located at the anterior end of the testicle. This is known as *Bidder's organ*. If the testicles of a young male toad are removed, the organ of Bidder will develop after 2 or 3 years into an ovary that secretes viable eggs. In other words, castration in this species throws the sex clear over to its opposite. Experimental work has also demonstrated that, in poultry, removal of the functional left ovary from a young chick causes the bird to develop the sex plumage and characters of the male, though it eventually returns to its original character. This is apparently due to the fact that the rudimentary right "ovary," in the absence of the suppressing effect of the ovarian hormone, develops into a testislike organ with seminiferous tubules in which some investigators report normal spermatogenesis. Occasionally, reports are circulated concerning hens that have changed into roosters and actually sired offspring, and the case reported by Crew is apparently an authentic case of sex reversal in the fowl.

In the higher mammals, sex is established at time of fertilization, and sexual differentiation begins fairly early in embryonic development. The young embryo has the primordia for either sex, and its genetic make-up determines which one will develop. The mechanism, genic, hormonal, environmental, sometimes fails to function perfectly and pseudohermaphrodites are produced. These are of various sorts; *i.e.*, both the male and the female embryonic primordia have developed to varying degrees from slight variations from one sex or the other to practically equal development of both sexes, but perfect in neither. Pseudohermaphrodites are more numerous in goats and pigs than other farm animals, and a few cases are known in man where one gonad developed into a testis found in the scrotum, the other into an abdominally located ovary. The external genitalia are also abnormal. Whether these aberrations are genetic or developmental is generally difficult to determine, but many no doubt do have a genetic basis.

In higher mammals once normal sexual development has occurred, complete sex reversal would be extremely unlikely. In the human, however, the secondary sexual characters of either sex sometimes appear in members of the opposite sex. Adrenal tumors have been shown to be

responsible for excessive growth of facial hair and the appearance of other masculine characters in the human female. Males subjected to certain estrogenic substances or males suffering from certain types of carcinoma may exhibit marked mammary development.

In the chicken following normal sexual development and egg production in genetic females, the atrophy of the functional ovary and the development of the ordinarily rudimentary right gonad into a sperm-producing organ is not uncommon. When this phenomenon occurs, the secondary sexual characters of the female regress and there is development of the comb and spurs, and crowing, treading, and other evidences of male behavior are common. A few cases have been reported in which such individuals have apparently sired chicks.

Numerous attempts to alter the sex of developing embryos by hormone treatments have been made. It has been possible to alter the morphology of the sexual organs, but complete experimental sex reversal is yet to be achieved.

Conditions Influencing Sex Ratio.—With sex evidently determined by the interaction of genes in the sex chromosomes and others in the autosomes and with one sex or the other (varying in different species) being heterogametic, we would expect generally to find an equality of numbers between the sexes provided there is equality of numbers and viability of the heterogametic sex cells, no selectivity between germ cells of the two types, and no differential embryonic mortality between the sexes. Nevertheless, the sex ratio is not always 1:1. Variations from the numerical equality of the sexes may conceivably be due either to genetic or environmental causes.

Genetic variations have been found in Drosophila. One of these behaves as a sex-linked and sex-limited-to-male gene that, when present in a male, either prevents the Y-bearing spermatozoa from being formed in numerical equality or lowers their ability to reach and fertilize the egg, for the offspring of such males have 96 female:4 male offspring. Even in the homozygous form, it apparently produces no ill effect in the female. Various lethal and semilethal sex-linked mutants are known in Drosophila, some of which kill only the females, because the Y chromosome carries the normal allele. Lethals in the autosomes sometimes give rise to peculiar sex ratios. In some interspecific crosses, no males or a greatly reduced number is born; in others, the reduction comes in the females.

Environmental conditions are also known that have an influence on the sex ratio. Seiler has shown that temperature affects the extrusion or retention of the X chromosome in a moth (*Taeloporia tubulosa*) in which the female is heterogametic. Season of breeding has been reported by

many authors to have an effect on the sex ratio produced, as have also time of breeding during heat, age of parents, etc., but these contentions are not well-supported.

Effect of Selection on Sex Ratio.—King's work with the albino rat illustrates the way in which selection may influence the sex ratio. This investigator, starting with two pairs of rats from the same litter, inbred litter brother and sister for 25 generations. With no selection from a sex standpoint in the first six generations, the sex ratio was 108.6, compared with a norm of 105. After the sixth generation, selection was made along two lines, *viz.*, the *A* line taken from litters with an excess of males and the *B* line taken from litters with an excess of females. The sex ratios were as follows:

TABLE 28.—SEX RATIOS IN KING'S INBRED RATS

A-line female × *A*-line males	122.3
B-line females × *B*-line males	81.8
A-line females × stock males	115.6
B-line females × stock males	91.1
Combined data for the two inbred lines	102.7
Stock females × *A*-line males	102.3*
Stock females × *B*-line males	96.2*

* Not significant statistically, according to King.

These results indicate that the sex ratio may be changed by selection, inasmuch as the straight inbred lines *A* and *B* differ from the norm by 17.3 and 23.2 points, respectively, but no wholly satisfactory explanation of the results has been devised. Miss King suggested that they might be due to differences in chemotactic attractions between ova and spermatozoa. Differential mortality rates between the two types of spermatozoa or the embryos arising from them might also be involved. Recent analysis of swine data indicates that inbred lines of swine differ significantly from each other in sex ratio.[1]

Any livestock breeder can cite instances of certain individuals, both male and female, that have tended to produce offspring preponderantly of one or the other sex. At the National Dairy Show in 1923, there was exhibited Financial King's Interest, a twenty-three-year-and-nine-month-old Jersey cow that had produced 21 calves, 20 heifers and 1 bull. The records at the Massachusetts State College show a Guernsey bull that left 28 bulls and 14 heifer calves, a Holstein that left 26 bulls and 19 heifers, an Ayrshire that left 18 bulls and 7 heifers, and a Jersey that left 11 bulls and 6 heifers. These are the most extreme cases that can be found in this dairy herd over a period of about 15 years. Among

[1] VERNON, E. H., *Jour. Anim. Sci.*, **7**:516–517, 1948. (Abs.)

the cows 3:7, 2:6, 7:0, 7:1, and 7:2 combinations are the most extreme. The cows, as a whole, have produced 471 male and 452 female offspring.

Whether the tendency to produce more males or females runs in families, *i.e.*, has a genetic basis, has not been proved, and, if it were proved, the introduction of another male might lessen or reverse the tendency. A breeder is often faced with the practical problem of having a male that seems to sire a preponderance of male offspring, a bull that sires 16 bull calves in a row. Shall the breeder sell this animal and try again, or is the tide about to turn toward a sequence of heifer calves? There seems to be no categorical answer to this problem, and as in so many other situations in breeding the only method is that of trying, and the best answer that of experience.

Conclusions Regarding Sex Determination.—The work herein reported seems to justify the conclusion that, in mammals, sex is determined by the type of spermatozoon that fertilizes a given ovum, and the paucity of knowledge concerning the factors that determine just what spermatozoon shall fertilize a given ovum must be admitted. It may possibly depend upon the chemical attraction between spermatozoa and ova. Those who argue that sex is dependent on the male are partly right, because the germ-cell differentiation in mammals occurs in the male; and those who argue that sex is dependent on the female may be partly right, because the ovum may possibly attract some spermatozoa more strongly than others. Unquestionably, chemical changes that affect the sex ratio do occur in both spermatozoa and ova, and the solution of the problem will result from a more thorough knowledge of both sexes, as, no doubt, they both exert large influence.

Sex Control.—Because the gametes differ in genetic make-up in respect to sex, it is quite logical that their differences may ultimately be measured by physiochemical, immunological, microscopic, or other techniques. As yet, it cannot be said that the gametes can be separated on the basis of their sex potentials or that sex can be controlled.

Literally hundreds of "systems" have been proposed for the control of sex. Most of these have not been subjected to analyses for testing their significance, and when statistical analyses have been made, none of the methods yet proposed has been shown to provide a reliable and practical method for the control of sex.

Some livestock breeders believe that there is a relationship between the time of service in relation to the onset of heat and the sex of the offspring. There is such a relationship between time of mating and level of fertility, but in view of present data, it does not seem likely that the length of time which sperm remain in the female genitalia prior to ovulation has any influence on sex. Other livestock breeders have associated sex control

with ovarian activity. The idea that one ovary produces ova which give rise to males and the other to females has been proposed. The obvious fallacy that mammalian sperm rather than ova control sex negates this belief. The possible role of the female in the determination of sex persists because of the not uncommon observation that some individual females have offspring of predominantly one sex.

It is difficult to trace the exact origin of the hypothesis that the reaction of the female genitalia, usually expressed in pH, influences sex. There are numerous variations of the general idea that an alkaline reaction produced by douching will result in a prepondernace of males and an acid reaction in the production of females. Although some data have apparently indicated that the expected sex ratios have deviated somewhat from the normal, the consensus of opinion seems to be that sex cannot yet be controlled by such techniques. It is well known that the secretions in the various parts of the female genital organs are well buffered and that douching the vagina, for example, will have little or no effect on the remainder of the tract. For this reason, some investigations have been made on the alteration of the pH of the semen. To the authors' knowledge, the exposure or storage of sperm at different pH levels has no significant effect on the sex ratio.

Because of the presence or absence of the X or Y chromosomes, it seems logical that there are physical or chemical differences in the sperm. It has been proposed that a separation of sperm on the basis of size might result in a separation of those of different sex potential. This idea has some merit, but it is obvious that a separation of the sperm cells on this basis has many practical limitations. It should be possible to accomplish this by centrifugation, and several mathematical calculations for such a separation have been made. It is entirely possible that centrifugation under highly controlled conditions might be effective. What effect this would have upon fertility and whether sex could be effectively controlled is hypothetical.

Still another, but not the last, approach is based upon the electrical charge of the sperm of different genetic make-up. It has been suggested that sperm of different charges could be separated by passing an electric current through a suspension of sperm. It has been reported that by sampling a charged suspension at the anode or cathode regions that the sex ratio has subsequently been altered. Although this idea is a relatively old one, it has not yet been sufficiently explored to warrant the conclusion that sex can be controlled by such procedure.

While effective sex control is far from realization in 1950, it seems possible that advances in the physical and biological sciences will eventually make possible the production of males or females at will, or will at

least alter the normal sex ratio. From the standpoint of practical livestock production, this would constitute a real advance in technology.

Summary.—The general role of the chromosomes in the determination of sex was substantiated in 1905. The two principal additions to the chromosomal theory since that time have consisted of the theory of "genic balance" between the autosomes and sex chromosomes and the more recent localization of the effective materials in the sex (X) chromosome to a known small region of this chromosome. We have lately come to understand more fully the part played by the endocrine secretions in sex differentiation among the higher animals as well as some of the conditions that affect the sex ratio and the possibilities of affecting the latter by selection. In spite of many attempts to solve it, the problem of controlling sex remains unsolved up to the present.

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[1] See lists at end of Chaps. XI and XII.

SECTION IV

The Art of Breeding

CHAPTER XVIII

SYSTEMS OF BREEDING—UNRELATED ANIMALS

We have now completed three sections of this text on animal breeding. The first section was designed to give the student an over-all view of the history and status of breeding at the present time as well as an introduction to the origin and relations of all living forms in terms of the probable physical basis of life and inheritance—the genes and chromosomes.

The second section dealt with the scientific and practical phases of reproductive physiology in order to acquaint the student with the fundamental procedures in the production of a new generation and to indicate the practical procedures that will best ensure a high degree of reproductive efficiency.

The third section dealt with the workings of the genes and chromosomes in the perpetuation of similarities and the creation of new types among related forms. Perhaps the student sometimes wondered why he should learn all the details of mono- and dihybrid crossing, of dominance and epistasis, of lethals, multiple alleles and multiple factors, of sex-linked and -limited inheritance, of linkage, crossings over, chromosome mapping, interference and limitation of the linkage groups, and of the various and sundry types of gene mutations and chromosomal aberrations, for it is so difficult to find examples of the actual working of these principles in the farm mammals. Knowledge of the basic principles, nevertheless, should be valuable in acquainting the student or breeder with the complexity of the problem with which he is dealing. He can rest assured that all these principles are at work in the germ cells of the animals in his herd or flock, although in most instances so many genes are involved, in such complex interactions, and so few offspring are produced that the result of the operation of any one principle is generally difficult, if not impossible, to measure.

Such knowledge should make the breeder approach his practical problem of creating better animal types in a less cocksure manner and with a greater realization that he is dealing with a complicated mechanism

which demands as full a knowledge of details as it is possible to achieve. In rebuttal, it might be argued that old-time breeders often achieved great success in total ignorance of the basic principles. This must be admitted, but we should be aware of the fact that less publicity has probably been given to those old breeders' failures. Their task was to create a few outstanding individuals, on which breeds could be built; ours is to raise the average merit of all our animals, which can be accomplished only if we fully understand the natural principles underlying reproduction and the mechanics involved in hereditary transmission.

This, the fourth and concluding section, will deal with the practical matters involved in livestock improvement—selection of animals for specific matings. Systems of breeding and selection constitute the only tools available to the breeder for animal improvement, since we cannot make any new genes but only, starting from where we are, arrange what we have or can buy into more desirable groupings.

Each breed of livestock, as now constituted, has as its genetic capital the complete reservoir of genes as they exist in the living members of the breed. Each breed has a certain number of good genes and a certain number of bad ones. If the number of good genes can be increased at the expense of the bad ones, the breed will progress. If the opposite result eventuates, the breed will retrogress.

Nearly all breeds are debarred by their own rules from going outside of their own limits for new genes. It cannot hope for any speedy progress from the natural occurrence of beneficial gene mutations, and there is at present no known way of creating helpful mutations through artificial means. Breed progress depends, therefore, on the relative gains in frequency of its desirable genes and possibly their recombination into more desirable groupings. New breeds can also be created, if and when that seems desirable or necessary, by combining characters, as they now exist in separate breeds, through systems of crossbreeding and selection followed by inbreeding.

An individual breeder, likewise, has as his genetic capital the genes existing in his living animals. He, of course, can augment this supply by purchase from other breeders. He usually does this through the purchase of males.

Before the breeds were formed as such and their books closed, a group of breeders in a region could and did go outside the not-too-distinct confines of their own type to get some genes that they desired. In getting these good genes, they also had to take some that they did not want. Their task was, therefore, that of so mating and selecting their animals that they might retain the good and discard the bad genes. It was in this fashion that our purebreds were formed.

The pool of genes in any breed has, in general, seemed to be elastic enough to permit the ideal to range between rather wide limits. At the beginning of this century the commonly accepted type of hog was short-legged, deep-bodied, and extremely rapid-fattening. Differential growth rates exist between the various parts as well as tissues of the body. In this "chuffy" type of hog the bone growth and muscle growth proceeded rapidly to their rather low upper limits, whereas the third phase, that of fat deposition, came into play early and had a high limit. The result was an early-maturing, fine-boned animal with a high proportion of fat to lean. This type of growth was highly favored also by the prevalent practice of feeding largely on corn. The consumer demand gradually shifted to a leaner type of animal. To meet this changed demand, breeders changed their selection ideal as well as their system of feeding. By the late twenties or early thirties, the selection ideal in hogs had shifted to the other extreme—that of an upstanding, rangy, relatively shallow-bodied, and lean type of animal. In these animals the bone- and muscle-development phases continue for a long time and have a high upper limit; the fat-deposition phase arrives late and has a low limit as compared with hogs of the early 1900's. Probably if a group of breeders of "chuffy" hogs in 1900 had been shown a picture of the "race-horse" type of 1930 and told that their job was to create such a type, their first reaction would have been, it can't be done. Due, however, to the facts that the market demanded a change and that the kind of genes necessary to produce such a change existed in the gene pool of all the breeds, the change was brought about in a remarkably short time and, in fact, the change went too far. Some physiological changes are very complex in their nature; they undoubtedly depend on the actions and interactions of a great many genes that probably act in large measure through the mechanism of the endocrine glands; and for their full expression they are dependent upon the environment, especially its nutritional phases. Similarly, the pool of genes in our present-type hogs undoubtedly contains enough of the genes for "chuffy" type to permit the reverse of the above-described change from "chuffy" to big type to be brought about should it ever be desirable to do so.

Another familiar example is the smoothing up of the type of our dairy breeds during the past 30 years. While average production has been improved, a far greater change has ensued in type also during this time. Some might and do argue that the change in production has been due most of all to better feeding and management. This argument can hardly be used to explain the change in type. Again it is evident that the pool of genes in the various breeds contained a sufficient supply of genes making for smoothness of topline, proper set of legs, body, and

udder capacity, and general quality so that conscious, directed selection for these things could be successful.

In one of our dairy breeds the byword among breeders 30 to 40 years ago was "the 30,000-lb.-of-milk cow." In practicing such selection, the genes making for higher fat test were automatically discarded, owing to the general negative correlation between high amount of milk and high butterfat test. But again there was seemingly enough of a supply of genes for higher test left in the general gene pool of the breed to make possible the raising of the butterfat test of the breed by at least ½ of 1 per cent, although such a change might cost something in milk production.

One of our breeds of cattle has followed two divergent lines of development, one for milk, the other for beef. The genes for beef are still present in the former and those for milk in the latter, so that these two strains could be made to mutually replace each other if there were any point in doing so. Similarly, it would still be possible to make any beef breed over into a milking breed and vice versa by means of selection and systems of breeding.

With the actual formation of the breeds and closing of the books, the door to the admission of new genes, except such as might occur naturally through gene mutation, was closed. From that point on breed progress became simply a question of manipulating gene frequencies.

The technique for doing this resides in selection. The breeds or breeders try to increase their stock of good genes by permitting those animals which have the greater number of good genes to leave many offspring while restricting the number of offspring of those which have relatively few good genes. The first task of a breeder becomes, therefore, that of devising methods for ascertaining the sort of genes which his animals possess. This calls for some sort of measurement and for record keeping.

In addition to selection the breeder has the use of the tool of breeding systems.[1] Some systems of breeding render the germ plasm more heterozygous, others make it more homozygous. Both selection and systems of breeding can be used to influence gene frequencies, and they are the only means available for doing so. Systems of breeding and selection are the most important problems with which the breeder must deal. They constitute the art of breeding.

It should be understood at the very beginning that there is nothing about any system of breeding which guarantees it to be a success, or, on the other hand, that foredooms it to failure. Popular articles some-

[1] The term *systems of breeding* is here being used in a somewhat restricted sense. Constant selection is a breeding system, as are also assortative and disassortative matings.

times portray the systems of breeding used by some breeder or the type of matings used to beget some champion with the implication that similar methods should be adopted by all and sundry. However, the fact that some successful breeder used linebreeding has no necessary application to any other herd or flock.

Similarly, a crossbreeding or an inbreeding experiment that turns out well (or ill) cannot be taken as a rigid standard of what will happen the next time or in some other group or class of animals.

The success or failure of any system depends entirely on the genes present in the animals concerned, plus of course the breeder's ability to mate and select intelligently.

All systems of breeding can be grouped under two categories, *viz.*, outbreeding and inbreeding. Outbreeding includes hybridization, grading, crossbreeding, and outcrossing; inbreeding includes linebreeding and closebreeding. Outbreeding is the mating of unrelated animals, inbreeding the mating of related animals. Now all animals on earth are related if there has been an evolutionary process, as the evidence seems to indicate; *i.e.*, anyone in Tibet or Tombouctou probably has come originally from the same parent stock from which we came and has a lot of the same genes that you and I have, since we all belong to the genus Homo. These so-called foreign peoples are related to us but not very closely. Since inheritance is a halving process, any ancestor in the fifth generation back of us means very little, since his or her inheritance has been halved five times before it got to us and, therefore, there is very little of it left. As an analogy, think of halving a dollar five times—first, halving 50 cents; second, halving 25 cents; third, 12.5 cents; fourth, 6.25 cents; fifth, 3.125 cents.

To provide ourselves with a practical working limit, we say that if any two animals of opposite sex have no common ancestor back through four or five generations of their pedigrees, they are unrelated and their offspring will be outbred. On the other hand, if a sire and dam have a common close-up ancestor or ancestors, their issue will be inbred.

This chapter is concerned with the various types of outbreeding.

Heterosis.—For a considerable time it has been realized that the mating of unrelated animals is likely to yield offspring of increased vigor. This phenomenon is called heterosis or hybrid vigor. The genetic reason offered to explain it is based on the fact that genes favorable to production are generally dominant over their opposites. Species or breeds develop somewhat different sets of favorable (dominant) genes, and they all have some unfavorable (recessive) ones. When the species or breeds are crossed, one parent may supply a favorable dominant gene to offset the unfavorable recessive one supplied by the other parent and vice versa.

The offspring, therefore, has a larger number of dominants than does either parent and is likely to be more vigorous. If one parent (male) was *AA bb* and the other parent (female) was *aa BB*, the offspring would be *Aa Bb*. Now if these female hybrids or crossbreds were mated to a male *aa BB* and those offspring to a male *AA bb* and this system continued, the proportion having at least one *A* and one *B* would soon level off to about two-thirds of those born. Heterosis is probably due in part to the heterozygous condition and in part to the presence of more dominant favorable genes, although what part each plays we do not know. Since the hybrids or crossbreds are more heterozygous, however, they cannot be expected to transmit so uniformly as purebred or inbred strains. The retention of heterosis in various crossbreeding systems depends, therefore, on the genetic merit of the purebreds used and on how favorable "nicks" result.

Hybridization.—The widest possible type of outbreeding is the mating of two distinct species, and a good example of this is the mating of the horse and the ass species to produce the mule or the hinny. It seems probable that the horse and the mule (also the zebra and the quagga) have come from common parent stock. In the dim past natural selection working on variation (recombinations, mutations, and chromosomal aberrations) began to separate them off into distinct species. The divergencies progressed so that now the horse and the ass are distinct species. They still have many genes in common, but they also have enough different ones so that they are recognized as distinct species. Up to now, however, their genetic divergencies, while enough to set them apart as distinct species, have not been enough to interfere with the fertilization of eggs of one by sperms of the other. Fertilization will take place and offspring (mules or hinnies) will be born, although the males resulting are apparently always sterile and the females quite generally so. Sheep and goats are also related (have arisen from common ancestors), but a little less closely than the horse and ass since, while fertilization between them will occur, the embryo does not reach full development, but is resorbed or aborted. Sheep and cattle have also come from common ancestors, but in them the divergence has progressed so far that even fertilization is prohibited.

There can be little question but that nature has used hybridization down through the eons of time to produce new species. Neither hybridization nor any other form of mating produces new genes, all that any of them do is to group the old genes into new combinations. New genes do occur through mutations, new combinations of genes do occur through the various systems of breeding, and the net result has been evolution.

Various Commercial Hybrids.—The *mule* is one of the best known hybrids in the United States. The mule is the result of crossing a jack (male of the ass family) on a mare (female of the horse family). This cross has been valued for many centuries. Fertile mare mules have been reported at various times, but the reports have not until recently been capable of absolute verification. In 1920, L. T. Branham of Montalla, Tex. reported that a mare mule in his possession, which had been bred to a jack, had dropped a living foal. The contention was supported by affidavits of the owner and some neighbors. The mare was loaned to the Texas Agricultural and Mechanical College and, after failing to conceive when bred to a jack in 1921, dropped a living stallion colt in 1923 as the result of being mated to a Saddle stallion the year previous.

Another fertile mule has been reported from Indiana.[1] When bred to a Percheron, she dropped a stud colt with no mule or ass characteristics. Still another fertile mule has been reported from Arizona.[2] This mule bred to a jack dropped a mule foal, and motion pictures were taken of the birth. This mule is said to have dropped one other foal previously. In the above, we have two cases of mare mules bred to jacks producing mule foals and two mare mules bred to stallions producing horse foals. Since the chromosome number in the ass family is thought to be somewhat larger than the 60 found in the horse, the inference in each of the above cases is that these mare mules occasionally produce an egg containing nothing but 30 horse chromosomes, all or essentially all of the ass chromosomes having been extruded in the polar body. These results indicate that these fertile mare mules actually function as mares as far as the genetics of their eggs is concerned. If all the horse chromosomes were extruded, these mules would function genetically as asses. No cases of this sort have yet been reported, and the possibility of securing a fertile hybrid strain of true-breeding mules is as remote as ever and would seem to be theoretically impossible.

The genetic pedigree of these offspring of mules illustrates the sampling nature of the hereditary process, for they should evidently be written

Offspring:
  Horse if by stallion
  Mule if by jack
    { Stallion or jack
        { Stallion or jack
        { Mare or jennet
    { Fertile mule (passed on nothing but horse chromosomes)
        { Stallion
        { This line of pedigree obliterated genetically from this point back

Fig. 130.—Pedigree of offspring of a mule.

[1] See *Jour. Hered.*, 1939, p. 549.

[2] See *Jour. Hered.*, 1939, p. 548.

The mule approximates more closely to the ass than to the horse in general characteristics.

The *hinny* is the reciprocal of the mule, being the result of a stallion-jennet cross. It is said to more closely approximate the horse in general characteristics. The hinny has never become popular or numerous.

The *zebroid*, a zebra-horse hybrid, is fairly popular in the tropics because of its docility and its resistance to disease and the effect of the heat.

Several hybrids in the genus Bos are fairly common. Of these one of the best known and most valuable results from crossing the zebu, or humped variety of cattle (Brahman), on ordinary cattle. Heterosis is evidenced and the zebu's resistance to ticks, fever, and various diseases is at least partially dominant. This cross is quite common in Brazil and seems to be gaining in popularity in the southern part of the United States, especially in Texas. More will be said of it later.

Bison and cattle belong to the genus Bos and are interfertile. Bison bulls are bred to domestic cows to produce this cross. Males are seldom born alive, owing either to their height back of the shoulders, which prevents their passing through the cow's pelvis, or to too great a quantity of amniotic fluid, and seem never to be fertile. Some of the females are fertile. The first cross, bison bull on domestic cow, is called a *hybrid* or *half-bred bison*. The second cross is made by using a domestic bull on the foregoing hybrid. The females resulting from this cross are mated to bison bulls and the offspring are termed *cattaloes*. Besides more rapid growth and greater vigor, the following advantages over cattle are attributed to the cattalo, *viz*., greater resistance to many diseases, including blackleg and Texas fever, higher dressing per cent, failure to run from heel flies and to drift in storms, lower feed requirement, and a greater ability to withstand lack of water.

Grading.—Breeds of animals arose by slow degrees from the general population of livestock by a process of selection. Along with better fleshing, milking, or other qualities, certain breed trade-marks, such as color of hair or wool, shape and set of horns, etc., were secured. By systems of mating (often involving quite close breeding) and a continuous discarding of animals that did not show the desired combination of characters, animals which would breed relatively true were finally secured. When this had been accomplished, the obvious best thing for the breeder without purebreds to do was to secure a purebred sire to use on his grade animals. Thus the breeding system known as *grading* came quite naturally into being.

Grading is the practice of using purebred sires of a given pure breed on native or grade females. Its purpose is to develop uniformity and

to increase productivity and quality in the offspring. The pure breeds are generally capable of producing these results because they have been selected for many generations for particular points and purposes within rather narrow limits and specifications. This does not mean that a purebred will necessarily effect an improvement when bred to grade animals, for, unfortunately, as is quite generally recognized, there are even at the present time a goodly number of inferior purebreds. The average purebred, however, will help to bring about uniformity and to increase productiveness in the average grade herd and can be used for this purpose. The first-generation offspring will carry 50 per cent of pure "blood." When these in turn are mated to another purebred sire of the same breed, the resulting offspring will carry 75 per cent of pure "blood," etc. After five or six top crosses of this sort, where one breed has been adhered to for the sires, the animals are, to all intents and purposes, purebred, though they are not eligible to registration. This is because the purebreds have certain definite distinguishing characteristics that breeders do not want to see disturbed. Such might occur if five or six top-crossed grade animals were admitted to registry, it being possible and probable that the grades would be carrying along some genes in their germ plasm for undesirable characteristics from the standpoint of the pure breed which would, at some future time, crop out in the breed.

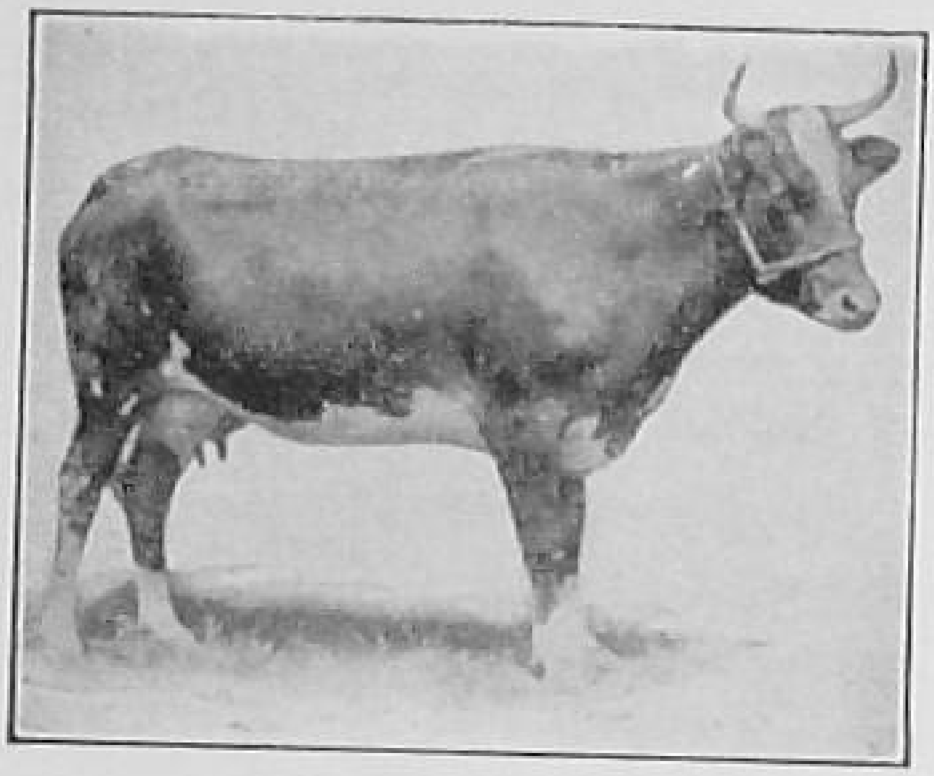
As the amount of pure "blood" approaches closer to 100 per cent, the grades come to look and behave more and more like purebreds, and they finally come to be practically indistinguishable from them. A native female has 100 per cent grade genes. Her offspring by a purebred sire has had one-half of its grade genes replaced by purebred genes. If one of these first-generation grade females is in turn mated to a similar purebred sire, its offspring will in turn have had one-half of its remaining grade genes (50 per cent of those it has) replaced by purebred genes, etc. We, therefore, would expect the greatest improvement in the first cross and less in each succeeding generation as the number of purebred genes is increased.

The fact that some grade animals outdo some purebreds has a tendency to lead some people to the erroneous conclusion that grading is better than pure breeding. Some purebreds have the genes that give them the external trade-marks of their breed but few of the genes for efficient production. Grading with this sort of purebred will not lead to rapid improvement, whereas grading with purebreds that have not only the external trade-mark genes but also a goodly supply of those causing efficient production will lead to rapid improvement. The majority of our animals are produced by grade breeding and probably will continue

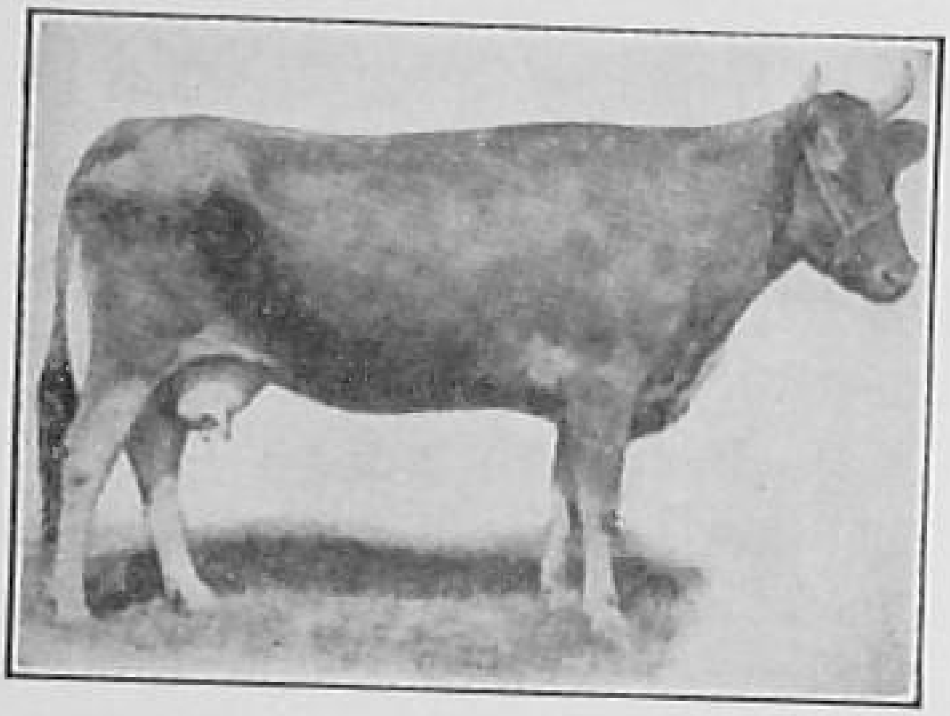
to be, as long as the average merit of the purebreds continues to excel that of the average commercial herd or flock. Here lies the real challenge to the purebred breeder to devise ways of ascertaining just what genes his animals do possess and also the means and the courage to rid his stock of poor genes.

One of the principal functions of the pure breeds is that of serving as a source of seed stock for commercial producers. The commercial producer depends upon the purebred breeder to supply him with concentrated doses of good genes, which in turn means that the principal task of the purebred breeder is that of ridding his stock of poor genes. With such a double-barreled system in full operation, it would seem logical to advise the average man starting in the livestock business to start with the system of grading. It will be admitted at once that this system leaves something to be desired, but it must also be admitted that it has its advantages. The most important consideration is, no doubt, that of cost. With grades, a start can be made for considerably less money than would be required for purebreds. Breeders of purebreds recognize that this practice is sound and advantageous to them, for it will furnish a market for all of a breeder's really meritorious males and for his relatively few excess females, most of which he will need to keep and test. It will mean more business eventually for breeders of purebreds to have beginners start with a grade herd and a purebred sire and later, when they have learned something of the business and have become established, change over to a purebred basis. If beginners are induced to start with purebreds, the herd must be a small one because usually the capital at hand is limited and the opportunity for eventual success and growth in the business is thereby greatly curtailed. Many men have started with purebreds, have soon become discouraged, and either have gone back to grades or have gone entirely out of the livestock business. Besides the greater initial cost of starting with purebreds, there is another influence to consider, *viz.*, that when a man has invested in purebreds, he is quite likely to think that he ought either to sell all his herd increase at rather high prices or to retain it in his own herd as breeding stock. This is an element that hurts the purebred breeding business in many ways. In the first place, all the increase of these herds is not capable of improving the breed, and a part of it should go to the packer. The average man will not hesitate to send surplus off-type or low-producing grade offspring to the butcher, but it takes more courage than some men possess to see the offspring of purebreds, for which they have paid considerable money, going that way. For purely commercial purposes, a herd of good grade animals, headed by a good purebred sire, is just as efficient and will make the owner as much money as a herd of purebreds.

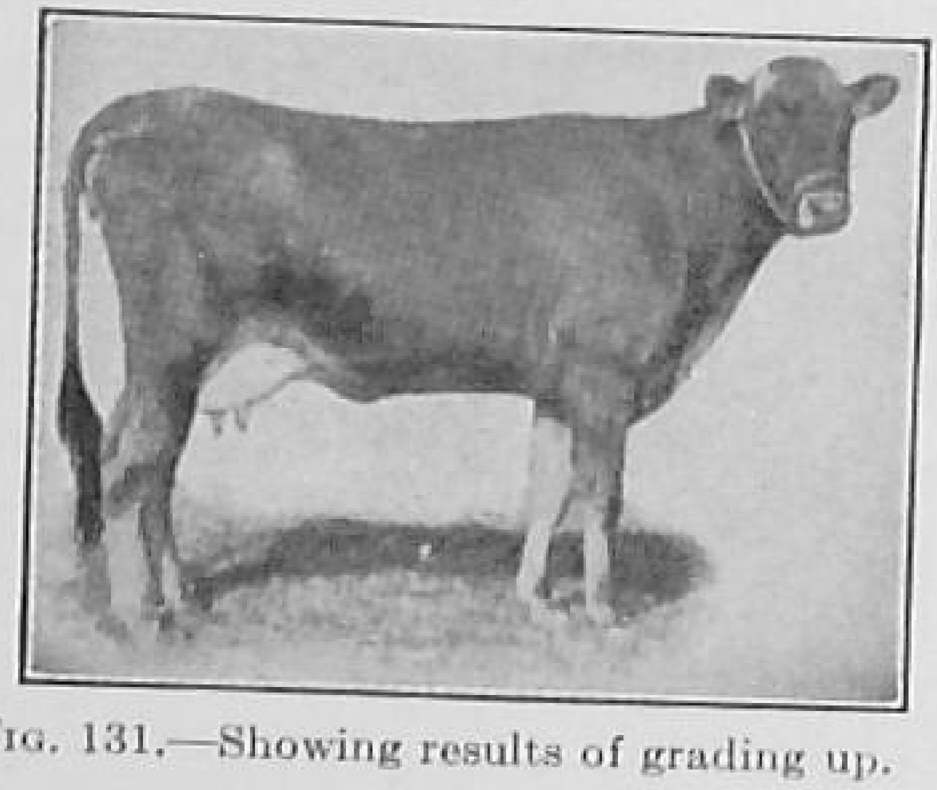
For the young breeder, it is a serious question whether to start with purebreds or grades. Many arguments can be advanced on both sides, and in the final analysis it is a matter to be settled individually. It would no doubt often be possible to start with somewhat old, timeworn



Scrub cow No. 60. Average production 3,313.2 lb. of milk and 178.47 lb. of fat.



Half-blood Jersey No. 241 out of scrub No. 60. Average production 6,126.4 lb. of milk and 348.98 lb. of fat.



Three-quarter blood Jersey No. 348 out of half-blood Jersey No. 241.

FIG. 131.—Showing results of grading up. (*From Iowa Agr. Expt. Sta. Bul.* 188.)

purebreds about as cheaply as with grades. A prospective breeder might find that he could secure individuals that were growing old, cows with only three good quarters, etc., for the same prices he would have to pay for grades. If such animals were of good blood lines, had no hereditary defects or unsoundnesses, had a reasonable prospect of producing a

few more offspring, and could still produce enough so that they would yield a little more than the cost of their keep, they no doubt would prove to be profitable investments. Young breeders of limited means who plan eventually to have purebreds may well consider this and somewhat similar plans for getting good "blood" (good germ cells) at reasonable prices.

McCandlish, Gillette, and Kildee, at the Iowa Agricultural Experiment Station, graded up a herd of scrub cows with purebred sires of the

FIG. 132.—The grade Clydesdale gelding, Major MacFarlane, champion at the International 1921 and 1923. He is only two generations removed from a cayuse mare.

dairy breeds. The first-generation grades produced 55 per cent more milk and 44 per cent more fat than their dams, and the second-generation grades produced 116 per cent more fat than their scrub granddams, owing to the fact that these cows not only produced more milk, but had longer lactation periods, things for which the purebreds have been selected for a great many generations. The champion gelding at the International Livestock Exposition in 1921 and 1923, Major MacFarlane, was a grade horse two generations removed from a cayuse or Indian pony mare. The thousands of purebred beef bulls that have been used on the cattle of the Western ranges during the last half century have graded up these herds and greatly improved the quality of the carcasses produced.

The following[1] is the summary and conclusions following 10 years of grading up beef cattle at the Sni-a-Bar ranch in Missouri:

> The use of purebred sires of acceptable quality results in successive improvement in the quality of the calf crop, as shown by conformation and market price.
>
> The greatest single step toward improved quality, compared with common stock, occurs in the first cross. Subsequent crosses increase quality and market value still more, though in less marked degree.
>
> Quality and best market prices are approximately in proportion to the number of crosses of pure breeding.
>
> After the third or fourth cross the offspring compare very favorably with purebred stock in conformation and only exceptionally good sires can bring about further improvement.
>
> Steers sired by purebred bulls at Sni-a-Bar Farms have topped the market 16 out of 20 times and have 4 times been the highest for the year to date of sale on the Kansas City market for fat yearling beeves.
>
> Early maturity is a conspicuous result of beef-cattle improvement through the use of purebred sires.
>
> Steers raised at Sni-a-Bar Farms as a part of the demonstration have sold consistently for about $2 a hundred pounds more than the average of other cattle on the same market, and during the period of high prices in 1918 for as high as $5.95 a hundred above the market average.
>
> Show-ring results are in general agreement with market preferences so far as indicated by the successful showing of Sni-a-Bar stock in market classes and by sales of similar cattle on the market.
>
> The demonstration shows clearly that breeding is a dominant factor in the production of high-quality beeves and that good feeding and management will not return best results unless the element of good breeding is present also.
>
> In grading up farm cattle the quality of calves is approximately in proportion to the individual excellence of the sires used, hence the importance of selecting bulls possessing qualities sought for in the offspring.
>
> Attendance at the grading-up demonstrations has increased from about 500 persons in 1917 to 10,000 in recent years, indicating a wide public recognition of the practicability of raising better cattle.

Purebreds do not always effect improvement when used on grade or native animals. The reason for this may be genetic—lack of sufficient good dominant genes in the purebred, as already mentioned. It might also be due to environmental or environmental and genetic reasons. Purebred stocks which give good results in one set of environmental conditions do not always give favorable results in some different environmental milieu. Purebred dairy cattle from temperate zones often degenerate when used in tropical areas, and their offspring do not have the vigor and constitution for high production in the warmer climate.

[1] *U.S. Dept. Agr. Misc. Cir.* 74, 1926, pp. 26–27.

For grading to be successful, it is not enough to use good purebreds, but these purebreds must have evidenced the ability to perform well under the conditions which their offspring must meet.

It often happens that under grading-up systems the offspring receive better care than did their female parents. In this way merit which is environmentally caused is likely to be attributed to genetic worth of the males used. This same feature may be found in artificial breeding where the proved sires' offspring may tend to get better care than did their grade dams, thus falsely giving genetic credit to sires.

Crossbreeding.—Crossbreeding includes several types of matings. Most generally the term means the mating of purebred animals belonging to different breeds. It sometimes is used to describe the mating of animals belonging to different species, *e.g.*, the horse and ass cross resulting in mules and hinnies, but this might better be called hybrid breeding. Again the term *crossbreeding* is used to cover cases of mating purebred sires to high-grade females, but this actually is grading.

Crossbreeding brings together more or less divergent sorts of germ plasm and may result in considerable uniformity in the F_1 but may give rise to variations, especially in the F_2 and subsequent generations. In this, as well as in the matters of size, vigor, and fertility, one or more of which crossbreeding usually increases, it is quite often the opposite of closebreeding. Crossbreeding has both desirable and undesirable features.

Crossbreeding is used to a considerable extent in the production of meat animals, because crossbred animals often show an increase in growth, vigor, and efficiency of feed conversion over either one of their purebred parents. Some of the grand champion steers at the International Livestock Exposition have been crosses among Herefords, Angus, Shorthorns, and Galloways. California Favorite, the grand champion in 1916, was a crossbred Shorthorn-Hereford and was reputed to have been one of the finest steers ever exhibited. A crossbred Shorthorn-Angus won in 1941.

Crossbred animals are often superior to purebreds in individual merit. Owing however, to their heterozygous nature, they often lack the ability to transmit breed trade-marks in a uniform manner. A Hereford-Angus crossbred will be black-bodied, white-faced, and polled and heterozygous for all three characteristics so that eight different combinations of these three pairs of genes will be found in such an animal's germ cells. If, however, the parental Hereford and Angus had the genes for desirable meat type, the crossbred would probably be of good meat type and would also transmit it.

A great many crossbreeding experiments have been carried out during the past 30 years. In March, 1924, a double litter of pigs was born at

the farm of the College of Agriculture of the University of Illinois. It was a double litter in that a Duroc-Jersey sow was mated to both a Duroc-Jersey and a Poland-China boar at one estrus. The resulting litter contained 10 pigs, 6 of which were Duroc-Jerseys, whereas the other 4 were spotted red and black and, therefore, evidently crossbreds sired by the Poland-China boar. The purebred pigs weighed 3.23 lb. each at birth, whereas the crossbreds averaged 3.75 lb. The pigs were all handled and fed in the same manner, and at six months the 2 remaining purebreds (females) averaged in weight 185.5 lb., whereas the 4 crossbreds

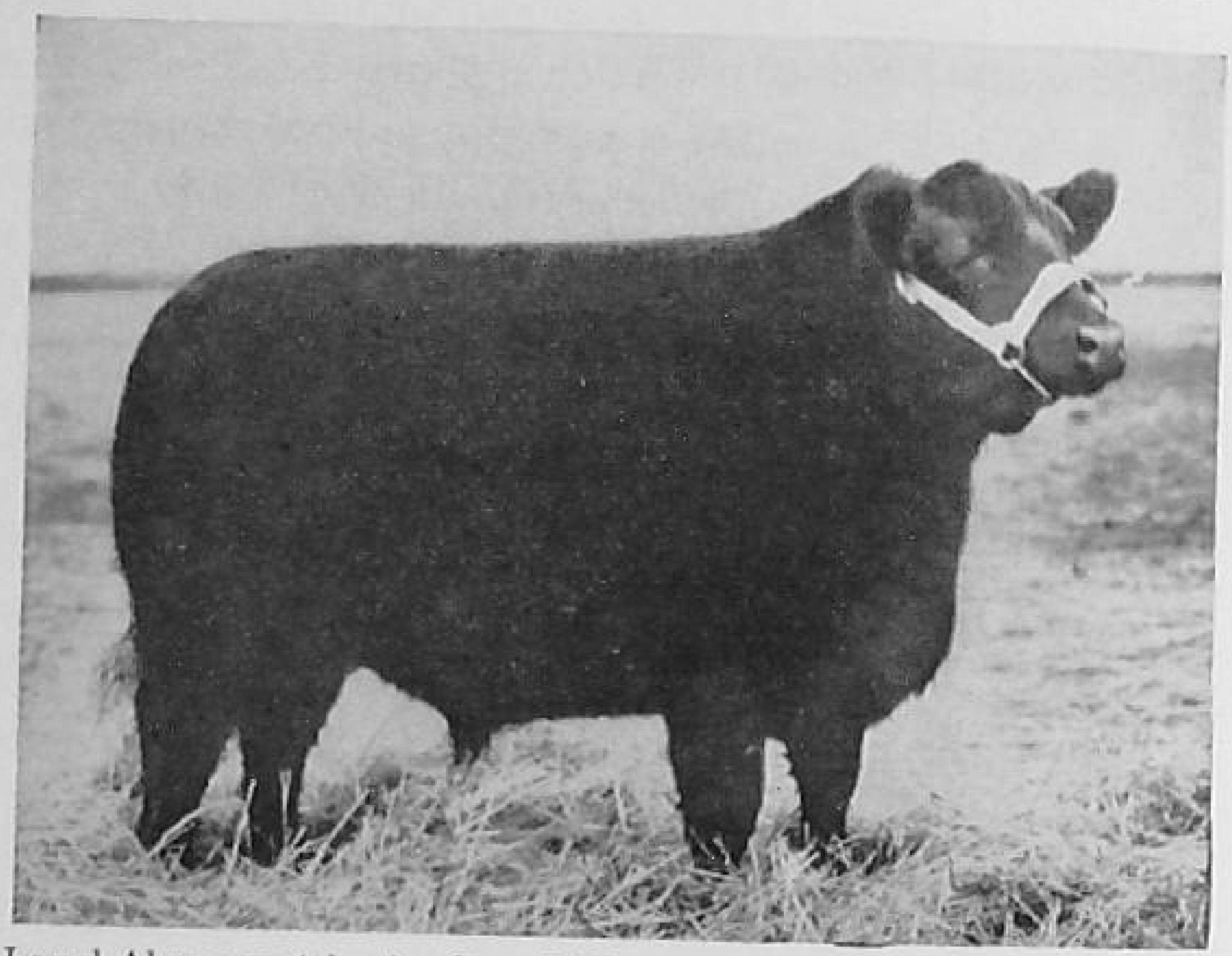


FIG. 133.—Loyal Alumnus 4th, the Grand Champion Steer at the 1941 International Livestock Exposition. This steer was out of a Shorthorn cow and by an Angus bull. (*Courtesy of Animal Husbandry Department, Purdue University.*)

averaged 235.2 and the 2 female crossbreds averaged 228 lb. This is a striking example of heterosis.

Roberts and Carroll carried on an experiment involving double matings of Poland-China and Duroc-Jersey sows to both Poland-China and Duroc-Jersey boars in which 5 crops of pigs and 105 litters were produced. Of these 24 litters were purebred, 16 crossbred, and 65 were mixed litters. Litter size for purebred litters was 8.0 pigs, for crossbred litters was 7.4, and for mixed litters was 9.8. All purebred pigs averaged 2.62 lb. at birth, all crossbreds 2.64. When paired for sex and in same litters, the purebred pigs weighed 2.63 lb. at birth, the crossbreds 2.76. There was little difference in strength at birth between purebreds and crossbreds judged subjectively. The mortality before vaccination (average age 38 days) was 43.3 for the purebred pigs, 41.1 for the crossbreds. Paired purebreds and crossbreds from 20 litters were used in feeding tests with

the following results in pounds: initial weight, purebreds, 65.3; crossbreds, 68.4; average daily gain, purebreds, 1.59; crossbreds, 1.65; last weight at same age, purebreds, 179.1; crossbreds, 185.6. The following[1] is the summary of this work:

Double matings were used with Duroc-Jersey and Poland-China swine to produce litters that contained both purebred and crossbred pigs.

A significantly larger number of pigs were produced in litters sired by two boars (mixed litters) than in litters sired by a single boar (purebred or crossbred litters).

The birth weights of purebred and crossbred pigs were subjected to three methods of analysis to determine whether the differences between them were significant. By the method considered best adapted to the problem, a small but significant difference in favor in the crossbreds was demonstrated.

Among pigs farrowed alive the strength gradings were slightly in favor of the crossbreds, but a slightly larger percentage of crossbred pigs were farrowed dead.

Mortality before vaccination was slightly less in crossbreds than in purebreds.

Small differences in favor of crossbreds were found in respect to weight at beginning of feeding test, daily rate of gain, feed per 100 lb. of gain, and weight near market age, but these differences were not satistically significant.

TABLE 29.—PUREBRED-CROSSBRED COMPARISON*

	Litters	Pigs	Weight, birth	Number weaned	Weight, 70 days	Daily gain	Feed, 100-pounds gain
Purebred Yorkshires	38	10.6	2.40	7.6	38.4	1.21	375
Purebred Chester Whites	36	9.8	2.38	6.6	39.4	1.30	403
York. male × Chester White female	29	9.9	2.49	7.4	42.7	1.35	371
Chester White male × York. female	29	10.1	2.42	8.0	42.8	1.33	370

* From *Iowa Agr. Expt. Sta. Bull.* 380.

Crossbreeding between Chester White and Yorkshire swine at the Bureau of Animal Industry Farm at Miles City, Mont. is summarized in Table 29.

If we average the above figures for the purebreds and for the crossbreds, we find that the crossbreds weaned 8 per cent more pigs which weighed 11 per cent more at 70 days and gained 7 per cent more per day up to market weight on 5 per cent less feed than the purebreds.

[1] ROBERTS, E., and CARROLL, W. E., A Study of Hybrid Vigor in a Cross between Poland-China and Duroc-Jersey Swine, *Jour. Agr. Res.* Vol. 59, No. 11, 1939.

The Iowa Experiment Station reports as follows on 108 litters of crossbred pigs from the Duroc-Jersey, Poland-China, Yorkshire, and Landrace breeds: (1) fewer stillborn pigs, (2) crossbreds more vigorous at birth and more reach weaning age, (3) crossbreds 3 to 4 lb. heavier at weaning, (4) crossbreds gained 0.09 to 0.12 lb. more per day, (5) crossbreds saved 10 to 14 days in reaching a weight of 225 lb., (6) crossbreds saved 25 to 30 lb. of feed in reaching 225-lb. weight.[1]

The crossbred sows observed in this study proved to be efficient pig producers, either when mated back to a boar of one of the parent breeds or to a boar of a third breed. When sired by a purebred boar the pigs from the crossbred sows, either backcross or three-breed cross, compared favorably with the first-cross pigs.

There is some general reason to suppose that breeds differ in their response to crossing and also that families or strains within breeds differ, but not enough evidence to determine which breeds can be expected to cross best with each other, nor whether distinct families which cross better than others exist and can be identified and maintained within pure breeds.

Crossbreeding can be continued as a steady policy only by going to purebred herds for the boars needed for replacement. Crossbred animals have a lower value than purebreds as transmitters of inheritance. Crossbred sows may be used successfully for breeding if the boar is a purebred. In this way the hybrid vigor of the crossbred dam in nursing and rearing pigs may express itself enough to more than compensate for her lower value as a transmitter of inheritance. No such offset for his lowered transmitting value could exist in the case of a crossbred boar. Planless and unsystematic crossing may quickly result in a mongrel herd from which the owner will get neither profit nor pride of ownership.

Carroll[2] and Roberts have analyzed reports on crossbreeding from the U.S. Department of Agriculture, nine state agricultural experiment stations, and six foreign countries involving over 50,000 animals. They measured hybrid vigor in the aspects shown in Table 30.

Carroll and Roberts took the following as their point of reference, "For crossbreeding to be judged beneficial, the performance of the crossbreds must excel the performance of the better of the two parental strains of purebreds." Only in one item "average daily gain" did this happen by 0.006 lb. per day. We think it fairer to compare the purebreds with the average of the parental breeds as is done in Table 30 right-hand column. In five of the six items the crossbreds are slightly better than the average of the purebreds.

A triple-crossing experiment with beef cattle has been carried out by

[1] Lush, J. L., Shearer, P. S., and Culbertson, C. C., Crossbreeding Hogs for Pork Production, *Iowa Agr. Exp. Sta. Bull.* 380, 1939.

[2] Carroll, W. E., and Roberts, E., Crossbreeding in Swine, *Ill. Agr. Exp. Sta. Bull.* 489, 1942.

Table 30.—Analysis of Crossbred Swine
Adapted from Carroll and Roberts

	Larger purebred	Smaller purebred	Crossbred	Av. of purebred parents	% by which crossbreds excel av. of purebreds
Size of litter....	1,538*—10.1 lb.	1,081— 9.4	1,515— 9.5	9.75	−2.5
Av. birth weight.	1,728 — 2.90 lb.	4,176— 2.65 lb.	6,137— 2.79 lb.	2.775 lb.	+0.6
Survival ability.	8,288 —80%	15,874—72%	9,935—80%	76%	+5.3
Weaning weight.	15,522 —33.4 lb.	8,133—31.7 lb.	9,519—33.3 lb	32.55 lb.	+2.3
Av. daily gain..	489 — 1.43 lb.	574— 1.319 lb.	794— 1.436 lb.	1.3745 lb.	+4.3
Economy of gain.	346 —366 lb.	274—382 lb	591—368 lb.	374 lb.	+1.6

* First figure in each column shows number of pigs involved.

Knapp, Baker, and Clark of the U.S. Range Livestock Experiment Station in cooperation with Montana Agricultural Experiment Station. Random-selected Hereford cows were mated to Shorthorn bulls, these females to Angus bulls, and these females to Hereford bulls, and the offspring tested against purebreds over a 2-year period for each cross. Five to eight purebred Hereford steer calves from each Hereford sire used were fed out against the crossbreds. Table 31 shows some of the steer data, more fully reported elsewhere.[1]

Table 31.—Triple Crossing in Beef Cattle

	1st generation av. of 2 years' results		2d generation av. of 2 years' results		3d generation av. of 2 years' results	
	Cross breds	Purebreds	Cross-breds	Pure-breds	Cross-breds	Pure-breds
No. of steers	57	67	24	91	20	161
Birth weight, lb	84.0	79.3	78.7	81.3	82.1	81.3
Weaning weight, lb	423	403	440	390	467	388
Final weight, lb	948	879	974	887	1,033	912
Daily gain per feed lb	1.92	1.75	2.00	1.86	2.32	2.10
Gain per 100 lb TDN, lb	18.3	18.0	17.4	18.3	18.9	19.0
Return above feed and marketing costs	$52.87	50.31	78.30	66.00	150.13	133.12

[1] Knapp, B., Jr., Baker, A. L., and Clark, R. T., Crossbred Beef Cattle for the Northern Great Plains, *U.S. Dept. Agr. Cir.* 810, 1949.

In the females, the weaning weight and weaning score of the crossbreds improved with each generation and all generations were superior to the purebreds. The weights of the heifers at 18 months were also in favor of the crossbreds. The first-generation crossbreds were the heaviest at maturity, followed in order by the purebred Herefords and the second-generation crossbreds.

Growth studies indicate that the first-generation females reach the heaviest mature weight, but up to 18 months of age the second-generation crossbreds were heavier than the first generation. The purebred Hereford females were the lightest of the three groups up to 5 years of age when they become intermediate in weight between the first- and second-generation crossbred females.

The calf-crop percentages as a whole were higher for the crossbreds than for the purebreds.

We assume that there was no selection in either group; *i.e.*, crossbred heifers were all kept to produce further crosses and the offspring of random-selected Hereford cows bred to random-selected Hereford bulls were saved each year to compare with the crossbreds.

The authors' discussion follows:[1]

The data presented indicate that all three generations of crossbreds were better in nearly every characteristic than the purebreds fed during the same year and handled as nearly the same as possible. In progeny groups from individual sires among both the purebreds and the crossbreds, considerable variation was found. For example, in daily gain in the feed lot, four purebred Hereford sire groups outgained the crossbreds and four others gained equally as well. Pure-bred-sire groups were also observed that weighed more at the end of the feeding period, that sold for as much per hundredweight, and that returned more money over feed and marketing costs than did the crossbreds. None of these superior bulls were used to produce crossbreds in the third generation because of their usefulness in another project.

Of eight bulls whose progeny on feed showed equal or superior gaining ability to the crossbreds, seven are from one inbred line that has shown superior merit in rate of gain. However, in the case of the three Hereford bulls used in both purebred and crossbred herds, the crossbred progeny materially outgained the purebred progeny from the same sire. The same statement applies to the Shorthorn bulls, based on tests at Beltsville. These results seem to indicate that the best results from crossbreeding are dependent on the procuring of good bulls, but indications are that the progeny of all bulls in this experiment performed better when out of females of a different breed than when out of females of the same breed as the bull.

For range producers of feeder cattle, crossbreeding has a distinct disadvantage that should be mentioned. Order buyers of feeder cattle tend to purchase steers of uniform breeding, type, size, color, and quality. Thus, crossbred cattle with

[1] Knapp, B., Jr., Baker, A. L., and Clark, R. T., Crossbred Beef Cattle for the Northern Great Plains, *U.S. Dept. Agr. Cir.* 810, 1949.

mixed colors are often discriminated against with a resulting lower price per hundredweight. The feeder buyer may be justified in his antipathy to off colors, because of the fact that inferior bred animals of poor fattening qualities may appear similar to the better bred crossbreds especially at the younger ages. Yet the finishing qualities of the two are sure to be different. It would seem, therefore, that unless the range producer is either selling direct to the feeder or producing grass-fat steers, the advantages of crossbreeding are largely lost on the feeder market. Such a disadvantage does not exist on the fat-cattle market where purchase is made on finish, quality, and killing yield.

The crossbred females were excellent range cows, high in fertility, and produced very heavy calves at weaning time. There seems to be a distinct advantage in crossbreeding from the female standpoint. The second- and third-generation calves appeared to profit as much from the fact that they were out of crossbred cows as from being crossbreds themselves. Milk production of the crossbreds was high yet it was not necessary to milk out any of the crossbred cows to prevent spoiling of the udders.

The conclusion seems sound that crossbreeding can be carried on most profitably where the range producer is able to crossbreed systematically and where he either feeds his own steers or sells direct to the feeder.

Commercial meat production can perhaps be carried on most easily and most profitably by crossbreeding provided good sires are used. For the purebred breeder to equal or surpass the results of crossbreeding, performance data must be collected and evaluated and relatively pure breeding lines be built up through close- and linebreeding.

Crossbreeding work with dairy cattle has been in progress at Beltsville, Md. by the Bureau of Dairy Industry since 1939, using Holsteins, Jerseys, Guernseys, and Red Danes. Since production data on the parental stocks was limited, practically completely lacking for the sires, it again is difficult to evaluate the degree of benefit from heterosis. Two-breed and three-breed crosses have produced very well. This could be anticipated if the parent females had a good hereditary complex to start with (genotype perhaps exceeding phenotype) and were to be mated to high-transmitting males down through the generations of crossbreeding. We would also anticipate good results from straightbreeding these cows to good sires of their own breed, in fact the Bureau of Dairy Industry has improved both their Holstein and Jersey herds from levels of over 600 lb. of butterfat to that of over 800 lb. by the use of a succession of proved sires in each breed. Good females (from good families) mated to good sires either in straightbreeding or crossbreeding will yield increasingly better offspring. Perhaps a slight amount in production will be gained by crossbreeding, but whether a crossbred dairy herd at the 525 lb. of butterfat level is worth more than a purebred herd at a 500-lb. level might be a debatable point.

Crossbreeding for the Market.—Next to grading, crossbreeding is used most extensively in the production of meat animals including poultry. Its greatest use up to the present has been with swine, less with sheep, and least of all with cattle and horses. In cattle a small amount of crossbreeding is practiced between Angus or Galloways and white Shorthorns to produce the blue-gray crossbred, between Angus and Herefords to produce black animals with white faces, as well as crosses between the beef and dairy breeds. Some beef ranches use a small proportion of bulls of another breed to utilize somewhat the principle of heterosis, whereas in some of the Gulf states a small proportion of Brahman blood is maintained in the cow herds to give added resistance to insects and disease. Crossbreeding has also been used in cattle for the purpose of studying the genetic mechanisms involved in the transmission of fattening and milking propensities.

Crossbreeding is also practiced quite extensively by range sheepmen by using rams of the Down breeds on grade Merino or Rambouillet ewes for the production of market lambs.

The most extensive use of crossbreeding has occurred with swine. One system is that of using purebred boars on purebred or high-grade sows of another breed. This often results in the production of faster and cheaper gains. The problems in this system are: (1) the continuing search for good sires (but this is true in all breeding) and (2) the problem of female replacements.

The rate of replacements will, of course, vary with different classes of livestock. With cattle the useful life of a cow probably averages between 4 and 6 years, which means that 16 to 25 per cent of the cows must be replaced annually, so that in a cow herd even with 100 per cent breeding efficiency, which of course is seldom achieved, one-third to one-half of the herd would have to be bred to a purebred sire of the same breed each year and all the resulting females raised in order to provide replacements at home. With ewes the length of the useful life is also about 4 to 6 years, so that a somewhat similar proportion of the flock must be bred pure each year, though this may be reduced somewhat if the percentage lamb crop exceeds 100. With sows the useful life is from 4 to 5 years, and, because they may be managed so as to produce six to eight pigs twice a year, the replacement problem is greatly simplified, for the replacements could be provided from one purebred litter each year.

For the production of market animals the crossbred females can be used for breeding purposes, thus making use of any gain in fertility and milking ability due to their heterozygosity. Workers at the Minnesota Experiment Station have suggested systems known as *crisscrossing* and *triple crossing*. In crisscrossing sows of breed A are mated to a boar of

breed B. Crossbred gilts from these matings are then selected and bred back to a boar of breed A, selected females from these matings being mated to boars of breed B, etc.

It is seen from Fig. 134 that the crossbreds under crisscrossing soon come to have about two-thirds of their blood from the breed of their immediate sire and one-third from the breed of their maternal grandsire. The Minnesota Station reports:[1]

The crossbred litters averaged from one-third pig to two pigs larger at weaning; on the average, each pig weighed from 5 to 7 pounds more at weaning, and the litters weighed from 39 to 96 pounds more than the purebreds. The crossbred

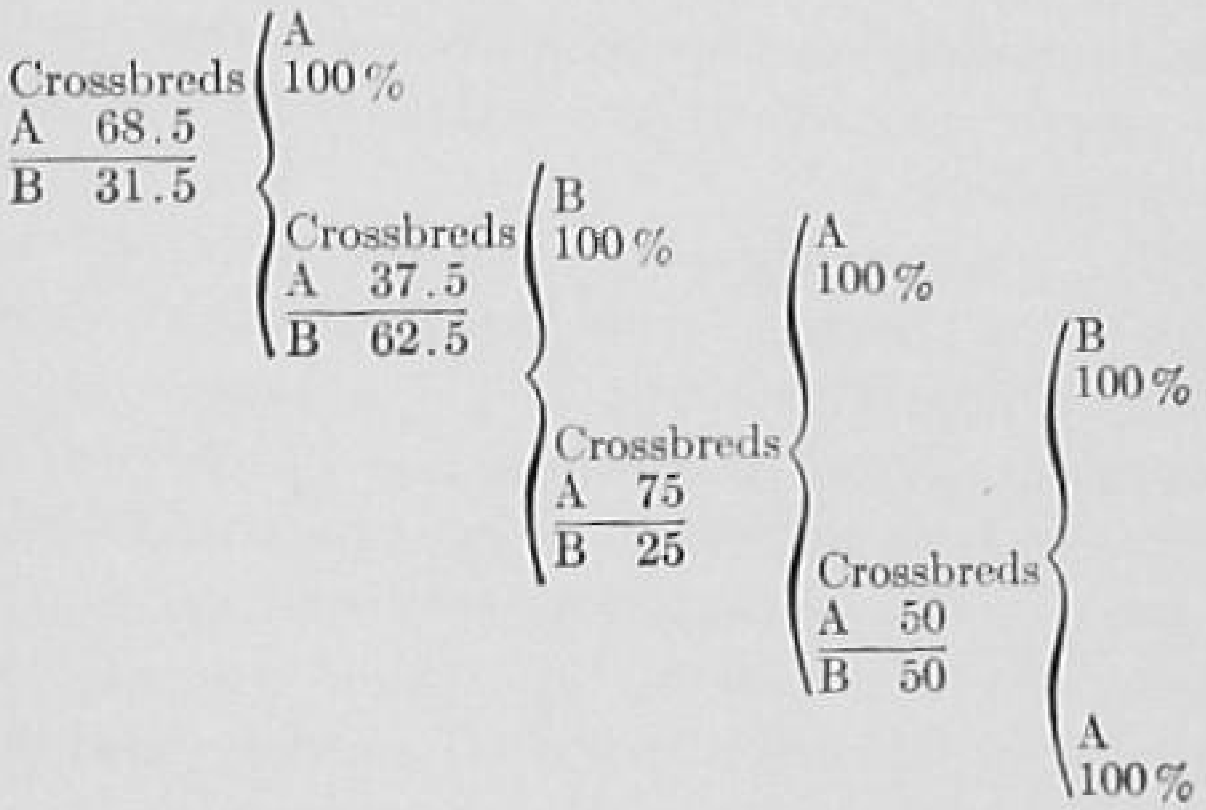


Fig. 134.—Diagram of crisscrossing.

pigs reached a market weight of 220 pounds from 17 to 22 days earlier than comparable purebreds, and they reached that weight on from 27 to 36 fewer pounds of grain.

Another system of continuous crossbreeding involves the use of three pure breeds and is known as *triple crossing*. As indicated in Fig. 135, the animals soon come to have about four-sevenths of their blood from the breed of their immediate sire, two-sevenths from the breed of their maternal grandsire, and one-seventh from the breed of the sire of their maternal granddam. Such a system retains heterozygosity in the animals and, provided the animals and breeds "nick" well, desirable results may be anticipated.

In both crisscrossing and triplecrossing, desirable boars of the two or three breeds must be located and purchased. The success of crossbreeding for the market (as indeed for any kind of breeding) hinges primarily on one's ability to secure purebred sires capable of introducing into the life stream the desirable hereditary determiners for vigor,

[1] *Minnesota Expt. Sta. Bull.* 320.

fertility, rapid growth, and good carcass qualities. We like to think of the bottom line of a pedigree as a stream that flows from female to female down the generations. If this is a pretty good stream to start with (good female family as determined by works, not faith) and the series of sires continually adds desirable genes, then the family, if sound selection is practiced, can get better as time goes on. This is equally true for crossbreeding or straightbreeding, be it noted.

There is some tendency to ascribe magic to crossbreeding, but there is none, nor in inbreeding either. All that any system of breeding can do is to put the genes now present in our livestock into new combinations. No system of breeding can make new genes—just new combinations of old ones. There is apparently some advantage in heterozygosity itself,

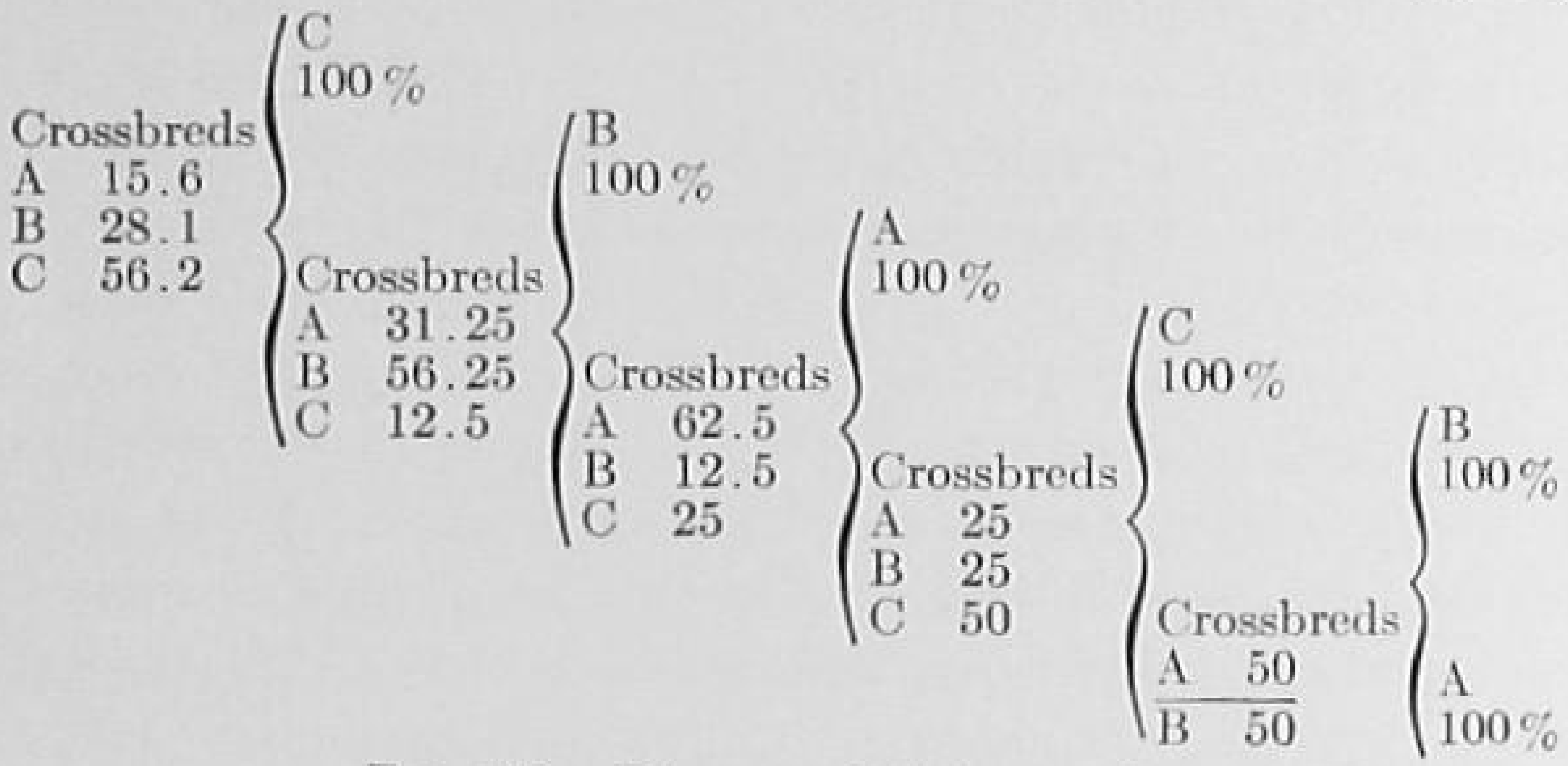


FIG. 135.—Diagram of triple crossing.

and the use of crossbreeding in commercial production of livestock products is steadily increasing. The growing realization of the need for good purebred sires for use in crossbreeding is both a challenge to the breeder and an assurance that his creations will be in high demand and at good prices. It will be most unfortunate for all concerned if crossbreeding comes to be considered a panacea for commercial meat production and the idea adopted that mating anybody's son of some breed with everybody's daughter of some other breed, or grades, would always give desirable results. Actually the value of crossbreeding lies in the genetic merit of the stocks crossed and whether the genetic complexes complement each other. We will not get any more out of a cross than we put into it, except a little in the way of interest.

The quick and widespread acceptance of artificial breeding in dairy cattle should provide the means for steady improvement in this class of animals. Formerly, we depended on purebred sires to effect improvement. However, all the sires of a breed would probably group themselves into a close semblance to a normal distribution curve if their transmitting powers could be measured. This means that 5 to 10 per cent of them are

very poor, 15 to 20 per cent are mediocre, 40 to 60 per cent are average, 15 to 20 per cent are superior, and 5 to 10 per cent are excellent in transmission. Under the old scheme of using purebred sires, so many were demanded that some rather poor ones were bound to be used. Artificial breeding still depends on purebred sires but makes it much more probable that fewer poor ones will be used.

It is being suggested that commercial dairymen with mixed-grade herds use semen from the best bull in the inseminator's kit on a given day when he has a cow in heat, rather than grading up to a certain breed by always using sires of that breed. We see no objection to this in principle. It will give the maximum in hybrid vigor. However, the dairyman will have to use some judgment as between sires in such matters as probable size of calf, milk yield, and fat test of cow to be bred, etc.

Crossbreeding and New Breeds.—Crossbreeding with its attendant variation, plus later painstaking selection and inbreeding, has been used for the creation of several new breeds. In sheep, the Oxford Down is the direct result of crossbreeding, the Cotswold and Hampshire Down furnishing the pure breeds for the cross. This crossing, followed by rigid selection for specific points and type, has established the Oxford Down as a pure breed. The Corriedale, a New Zealand breed of sheep, resulted from the use of Leicester and Lincoln rams on Merino ewes, and the Columbia breed was created by the specialists of the U.S. Department of Agriculture, using the Lincoln and Rambouillet breeds.

Two things should be borne in mind so far as the creation of new breeds is concerned. One is the fact that two men might start to cross breeds A and B to produce a new breed C. Since none of our breeds is entirely homozygous, they would surely start with different genetic materials. In addition, chance sampling of the hereditary material plus different ideals in each breeder's mind might result eventually in two samples of a new breed, called C, made up of very dissimilar genes and therefore very dissimilar in type and productive capacity. If they sold stock to other breeders, the two strains might further diverge. The other point to be kept in mind in the creating of new breeds is that of the time involved. Whether it is to take 6 generations or 16 or 60 before one would be justified in saying that the result of the original crossing and later selection now merits being called a new purebred is also an arbitrary matter. Many of the so-called new breeds still show a great range of variation after 25 or 30 years of careful selecting, and, as we have just stated, even the oldest of our pure breeds are still relatively heterozygous.

To the King Ranch of Kingsville, Tex., goes the honor of having created the first American breed of cattle, the Santa Gertrudis.[1] Estab-

[1] RHOAD, A. O., The Santa Gertrudis Breed, *Jour. Hered.*, Vol. 40, No. 5, 1949.

lished in 1851, the King Ranch was stocked originally with "Texas Longhorns" which had environmental fitness but yielded a poor carcass. Shorthorns and Herefords were used for top-crossing between 1880 and 1910 and successfully upgraded the carcass but downgraded environmental fitness. To restore the latter, recourse was had by Mr. Robert J., Jr., and Mr. Richard Kleberg to crossing with Brahman bulls, *Bos indicus*, after an exploratory period (1910–1918) indicated that the cross had promise. Three-quarter to seven-eighths Brahman bulls were secured from the Pierce Estate in Texas for mating with purebred Shorthorn cow herds. Red males and females from this F_1 were selected to beget the F_2 without inbreeding. One of the F_1 bulls (Brahman bull × Shorthorn $^{15}/_{16}$ to Brahman $^{1}/_{16}$ cow) was named Monkey and became the real

FIG. 136.—Santa Gertrudis steers in feed lot. (*Courtesy of King Ranch, Kingsville, Tex.*)

founder of the Santa Gertrudis breed. Because of the marked superiority of his calves, he was used extensively in breeding for a period of about 10 years, and 150 of his sons and later descendants have been used on the first-cross and double-cross cow herds. Planned inbreeding and linebreeding to Monkey plus some inbreeding to females has in 30 years yielded a new breed ($^3/_8$ Brahman and $^5/_8$ Shorthorn) combining environmental fitness and good carcass quality.

The Lasater Ranch of Falfurias, Tex., has developed the Beefmaster strain by using Hereford, Shorthorn, and Brahman blood. This program was started in 1908. The Lasaters make no claim to producing a new breed, their sole aim being to produce as good beef as possible under their conditions. These cattle are being tried out in other parts of the United States.

Turner and Thomas of Welaco, Tex., are developing a new beef breed called the Charbray through crossing the French Charollais breed with

Brahmans in the proportions of ¾ and ¼. These cattle are also being tried out in various parts of the United States.

The Hamprace hog has been developed at the U.S. Range Livestock Experiment Station, Miles City, Mont. by the Montana Agricultural Experiment Station and the Bureau of Animal Industry, U.S. Department of Agriculture, and is now generally referred to as Montana No. 1. Unbelted Hampshires and Danish Landrace provided the original stock. These strains were crossed and the breed developed by selection from the F_2 and backcrosses to each strain. For the 9-year period 1939–1947 inclusive, this new breed has averaged 10.6 pigs farrowed, 8.1 pigs raised,

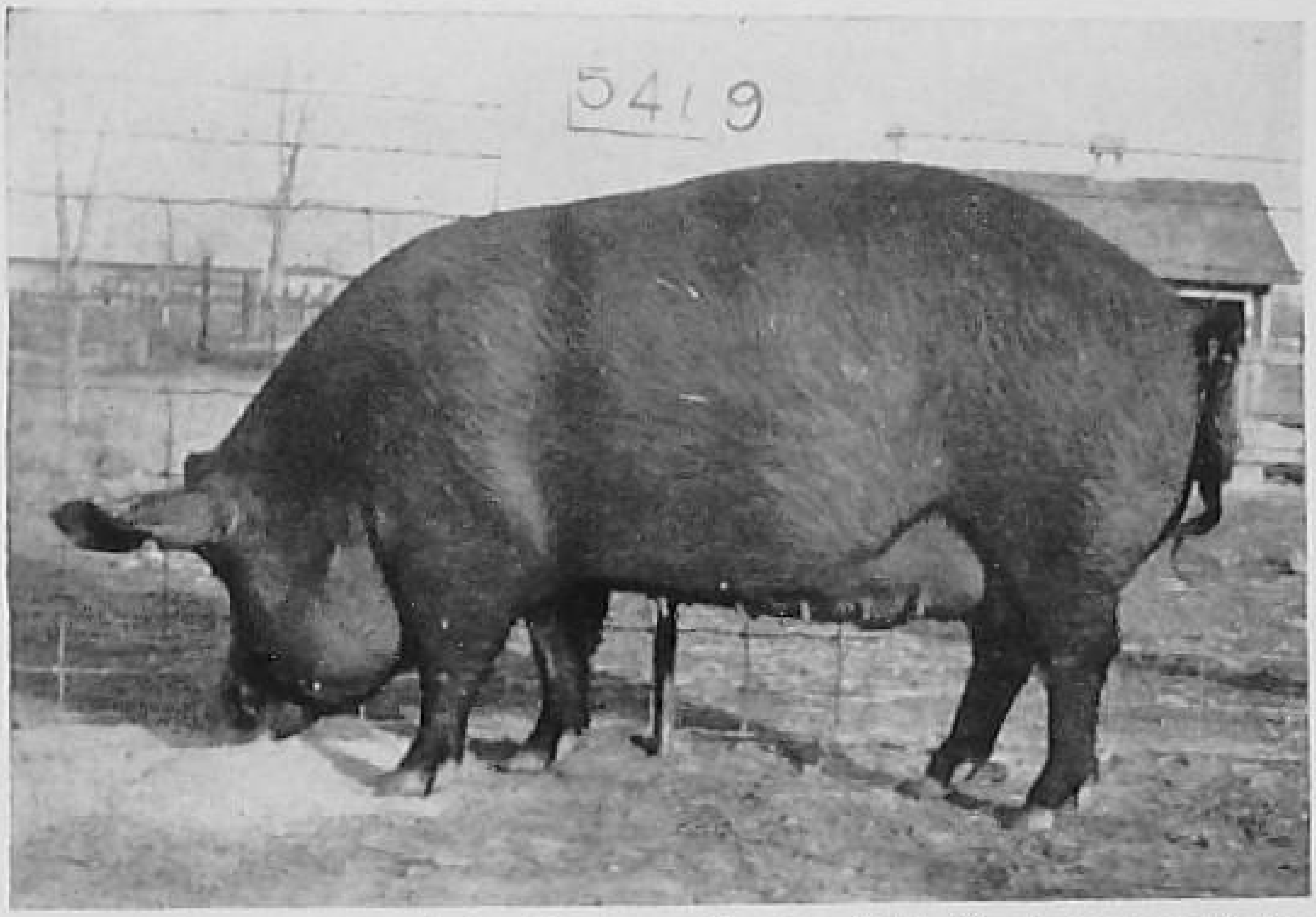


FIG. 137.—The grandmother of the Montana No. 1. This black sow was from a second-generation litter of the Landrace × Hampshire cross. In 8 litters she farrowed 96 pigs and weaned 83 at 56 days of age. The litters averaged 351 lb., or 34 lb. per pig. Selection has largely eliminated the depression behind the shoulders but has not increased productivity. (*Courtesy of J. R. Quesenberry, U.S. Department of Agriculture, Miles City, Mont.*)

with an average 56-day litter weight of 248.4 lb. Record of performance tests on an average of 68 pigs per year over a 5-year period showed an average daily gain of 1.43 lb. per day requiring 371 lb. of feed per 100 lb. gain, the latter showing a range of from 310 to 444 lb. Carcass tests on 48 hogs made at 184 days when the hogs reached 221 lb. showed a carcass length (aitch bone to first rib) of 30.4 in., the five primal cuts to average 47.1 per cent of the live weight and a backfat thickness of 1.5 in.

The Montana No. 1 is a solid black hog. The back is slightly arched. The sides are smooth and uniformly deep. The hams are thick and carry well down to the hocks. The legs are medium in length with a neat jowl. The ears are of fine texture, medium in size and vary somewhat in carriage, ranging from slightly erect to slightly drooping. The disposition is very quiet and docile.

The sows are quiet at farrowing time and suckle well. The breed is a good forager.

The Minnesota No. 1 and No. 2 are also new breeds—the former resulting from crosses of Tamworth and Landrace and the latter from crosses of Yorkshire and Poland-China.

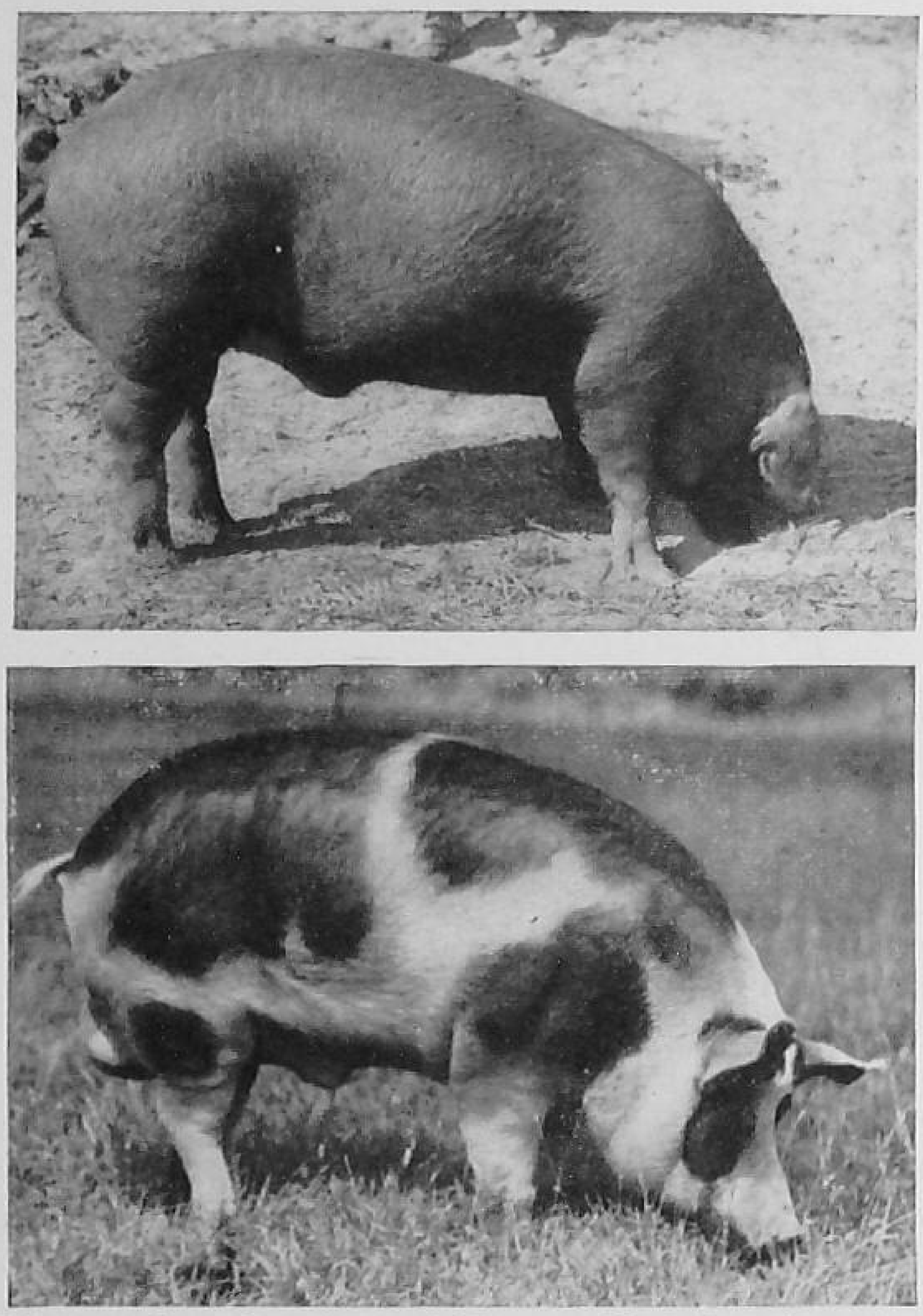


Fig. 138.—Minnesota No. 1, Boar (*top*) and Minnesota No. 2, Boar (*bottom*). (*Courtesy of L. M. Winters, University of Minnesota.*)

It should be possible through crossbreeding to establish new breeds with any desired combinations of characters, unless, of course, the latter are antagonistic to each other or certain genes are linked in such a way in the germ plasm that segregation is impossible. The drawbacks to this procedure are serious ones, however, because of the time and expense involved and the large number of animals that must be produced in

order to give ample range for selection. After these difficulties have been overcome, there would still remain even a greater one, *viz.*, selling the new breed to the breeders and growers, a matter which would vary among the different classes of livestock. The breeds as they exist today seem to fill most of the needs fairly well. Considerable variation still exists in all of our breeds, in fact, probably enough so that those in each of the classes could for the most part be made uniform in productive qualities through suitable matings and selection, although they would still differ in external character such as color, presence or absence of horns, set of ears, etc.

This whole matter of the possible creation of superior new breeds in any and all classes of livestock is an extremely fascinating one and has intriguing possibilities, though it is not a field in which an ordinary breeder with limited time, capital, and number of animals can hope to achieve success. He lacks the necessary equipment. If exploited at all, these fields should generally be left to the state agricultural experiment stations or the U.S. Department of Agriculture.

Uses of Crossbreeding.—Crossbreeding is useful in making genetic studies of hereditary transmission of characters. It provides the opportunity for combining the better genes of two or more breeds and thus getting enhanced commercial production. It offers the opportunity for the creation of new breeds by suitable crossing and selection followed by inbreeding to render the desirable combined genes relatively homozygous.

The practical breeder is generally not suitably equipped for genetic studies or for the formation of new breeds. These functions can best be carried on by experiment stations. He is vitally interested in the best methods of commercial production of various livestock products. Maintaining two or more separate breeds for commercial crossbreeding is not generally feasible, while mating crossed females to a series of good purebred sires of one or several breeds is. But there is no magic in crossbreeding, and promiscuous, planless crossbreeding is not likely to lead to beneficial results.

Finally, we should mention the aesthetic side of the problem. We all know of the pride that the good purebred breeder takes in his uniform, trade-marked flock or herd, sometimes bordering on biased, prejudiced partisanship. "Belonging" to a pure-breed association gives many men a deep feeling of satisfaction, and they can not only "belong" but also bathe in the reflected glory of the breed as a whole. For most men there probably is just more fun and satisfaction in working with a uniform flock or herd of purebreds than in working with grades or scrubs. As one farmer put it, "The extra five or ten per cent efficiency of a well-planned but heterogeneous group of grade animals is just not sufficient

compensation to pay me for what I lose in satisfaction by not having typical representatives of a well-defined, homogeneous group of purebreds."

Outcrossing.—The systems of breeding previously discussed in this chapter; *viz.*, hybridization, grading, and crossbreeding involve the mating of unrelated animals that do not belong in any one breed; in other words, they involve the uniting of very diverse bits of germ plasm. Outcrossing, on the other hand, is the mating of animals that are members of the same breed but show no relationship for at least the first four to six generations. As indicated in the early chapters of this book, it seems probable that all organisms extant and extinct which have ever lived on this planet are somewhat related. The theory of evolution suggests that all living things trace back to a single, or perhaps a few, similar origins. Cattle, sheep, and goats belong to the family Bovidae, *i.e.*, they have come through variation from the same progenitors. In the early stages of this diversification, the germ plasms were still compatible and the animals interfertile. Continued variation and selection among the genes finally reached the point where the germ plasm of cattle was not compatible with that of sheep, the animals, therefore, being sterile with each other.

So in the broad view all cattle are related and, of course, still interfertile. All cattle, in other words, probably have many genes in common. But for practical purposes, an animal that shows no common ancestor on both sides of its pedigree for four or five generations is called an *outcross*. To put it another way, when we mate two unrelated animals in the same breed, their offspring is called an outcross. The term *outcrossing* is also used to signify the selection of an unrelated male to use on a group of inbred females with the inference that the breeder will subsequently return to his inbreeding. It is used, in other words, to introduce some desirable genes into an inbred stock.

Most of our purebred animals are the result of outcrossing. The mating of unrelated animals sometimes results very favorably, to be sure, but it is also a fact that most breeders who achieve distinction do so by (1) securing desirable animals of certain strains or families in their particular breed and (2) intensifying the good characteristics of these animals through close- or linebreeding. Nevertheless, the master breeders at times have recourse to outcrossing for its regenerative effect or for the purpose of introducing new genes. Only when used in these latter ways with a specific aim in view is outcrossing to be commended.

Crossbreeding Effects within a Breed.—The good effects of crossbreeding are thought to be due not to the fact that breeds are crossed but rather to the fact that the genes making one breed good are somewhat different from those making another breed good. These two "goods"

when brought together often make something better than either one singly. In thinking of crossbreeding, therefore, we should think of genes rather than breeds. Since this is so, we could expect to find evidence of heterosis within a breed if selection and inbreeding had separated out different complexes of good genes. The Oklahoma Experiment Station working with the Regional Swine Breeding Laboratory reports such a case.[1]

The Oklahoma Station started a project with Duroc Swine in the fall of 1937. The project has been carried on in cooperation with the Regional Laboratory since that time. Four inbred lines of Durocs were developed. Line 1 had already been inbred in another project and was retained to be used in this project. It has been necessary to discard two lines to date and start two new ones. One was discarded because of a lack of fertility and the other one was discarded on account of inverted nipples. Moderate inbreeding is being used in this project. Most of the matings are half-brother × half-sister.

TABLE 32.—A COMPARISON OF 15 LINE CROSS LITTERS WITH PURE LINE LITTERS FROM EACH OF THE PARENT LINES, AND WITH CROSSBRED LITTERS

	No. of litters	Inbreeding of litters, %	No. of pigs per litter at		Av. weight of pigs at		Av. daily gains weaning to 6 months	No. of litters tested*
			Birth	6 months	Birth	6 months		
Pure line 1 1938–1943.....	62	39	7.8	3.3	2.3	111	0.72	10
Pure line 3 1938–1943.....	94	15	9.0	5.6	2.6	169	1.14	32
Line 1 X Line 3 Fall 1943......	15	0	9.4	6.2	2.4	199	1.38	10
Crossbreds, fall 1941 and spring 1942..	8	0	9.6	7.5	2.7	160	1.11	6

* A litter is tested by taking 4 representative pigs at weaning time and placing them in a small lot which has a concrete floor. The pigs are fed in this lot until they reach 225 lb. in weight. In case 3 pigs reach 225 lb. and the fourth pig is smaller, it is removed at the same time.

In the fall of 1943 fifteen litters were produced by crossing lines 1 and 3. Seven line-1 sows whose inbreeding averaged 39 per cent were mated to line-3 boars whose inbreeding averaged 28 per cent. Eight line-3 sows whose inbreeding averaged 25 per cent were mated to line-1 boars whose inbreeding averaged 36 per cent. While the inbreeding within the lines has not progressed very far, it was considered worth while to check the combining qualities of the lines especially since some preliminary crosses have shown promise.

[1] *Okla. Agr. Expt. Sta. Cir.* 113, April, 1944.

It seemed advisable to check the "line-cross" pigs with crossbreds as well as the pure line. Crossbred pigs were produced by mating line 1 sows to a highly inbred Poland-China boar from the Minnesota Experiment Station. The four comparisons made, "line cross," crossbreds, pure line 1, and pure line 3, are shown in Table 32. The line-cross litters were superior in about every respect to the better one of the parent lines. There was no difference in the economy of gains. The line-cross pigs gained faster from weaning time to 180 days of age. They were better in this respect than the crossbred pigs. The crossbred litters were a trifle larger at birth and a larger percentage of the pigs were raised to 180 days of age. Hybrid vigor seems to be manifested in the line-cross litters.

The average daily gains made by line-cross pigs during the fattening period were compared with the gains made by pure-line and outbred pigs. The line-cross pigs gained a quarter of a pound more per head per day than the outbred pigs.

The Committee on Investigations of the American Society of Animal Production, with W. V. Lambert as chairman, submitted the following report in regard to terminology to describe the progeny from various systems of breeding at the 1940 meeting.[1]

Crossbred. The progeny resulting from the mating of different breeds or, in the case of poultry, different breeds or varieties.

Incross. The progeny resulting from the crossing of individuals of inbred lines within the same breed, or variety.

Inbred Line. The progeny resulting from breeding closely related animals. To be classed as an inbred strain, the individuals should have an average coefficient of inbreeding of 37.5% (equivalent to 2 generations of brother-sister matings).

Incrossbred. The progeny resulting from the crossing of individuals from inbred lines of different breeds, or varieties.

Outcross. A cross of relatively unrelated animals within the same breed, or variety.

Topcross. The mating of a male of a certain family to females of another family of the same breed, or variety.

Topincross. The progeny resulting from the cross of inbred sires on noninbred dams of the same breed, or variety.

Topcrossbred. The progeny resulting from the mating of inbred sires with non-inbred dams of different breeds, or varieties.

Heterosis (or Hybrid Vigor). The superiority over the better parent that is exhibited by the progeny. This applies to the progeny from the crossing of strains, varieties, breeds, or species. The committee suggested that this terminology is sufficiently inclusive to describe various types of crosses without the use of the term "hybrid."

No decision could be reached on the term "hybrid" in view or the many different interpretations of the word.

[1] See *Amer. Soc. Anim. Prod. Proc.*, 1940, p. 378; and *Jour. Anim. Sci.*, 1(1):90, February, 1942.

Summary.—This chapter has dealt with outbreeding systems—all of which involve the mating of unrelated animals. All animals in truth are related, and the term *unrelated* was defined and limited to mean no common ancestors in the first four to six generations of a pedigree. The widest outcrossing is the mating of animals in different species—hybridization followed by grading and crossbreeding. The narrowest outbreeding system is outcrossing—mating of unrelated animals within one breed.

Outbreeding helps phenotype and hurts genotype or produces animals which in themselves are highly desirable but which cannot transmit uniformly. It keeps the genes heterozygous so that undesirable recessives cannot show up. Selection is not so necessary because there is no way of predicting what crossbred genotype may "nick" best with the next purebred sire.

Crossbreeding is a very useful system for the commercial producer—the animal multiplier. Outbreeding has possibilities for bringing together diverse kinds of germ plasm in the formation of new breeds. The form of outbreeding most useful for the constructive purebred breeder is outcrossing, and here the purpose is somewhat similar to that just mentioned, namely, the introduction of some new and missing genes into a purebred herd from another strain in the same pure breed.

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CHAPTER XIX

SYSTEMS OF BREEDING—RELATED ANIMALS

The last chapter dealt with the systems of breeding involved in the mating of unrelated animals, which were defined as those having no common ancestors on both sides of their pedigrees for at least the first four to six generations. It would be possible to bring to America 20 sows and 3 or 4 boars of some foreign breed and thus establish the new breed in America. The animals would become scattered to all parts of the country, somewhat different ideals of perfection might be set up in the different sections, and after thirty or forty generations there perhaps would be several thousands of animals in the breed. Most of the matings would then probably be between boars and sows that had no common ancestors in the first few generations of their pedigrees. Such matings would be called "outcrossing" although all the animals in this breed would trace back to some of the original 20 sows and 3 or 4 boars and would, therefore, be more or less related. Mutations, different selection ideals, and the sampling nature of the hereditary process would have made some of the sectional strains quite different genetically, although all the animals in the breed would probably have many genes in common. In fact, all living organisms are related, to some extent, from an evolutionary standpoint, and it is not inconceivable that all may have some genes in common.

Any two cattle of the present day trace back eventually to the few animals that through variation actually gave rise to the class of animals we now know as cattle. So much mutation, variation, selection, and recombination has transpired since that remote time that the fact that all cattle are of the same "blood" means little or nothing so far as their present genetic make-up is concerned.

It would be very interesting if you and I could throw on a moving-picture screen a parade of our ancestors, generation by generation, starting with our two parents, then following with our four grandparents, then our eight great-grandparents, etc. Occasionally, if all the facts were known about these people, we might be inclined to blush and would be reminded of a saying attributed to Mark Twain that "man is the only animal that blushes or needs to." If our parade extended back to

the time of Christ, there would probably be lots of duplications in it, since this would involve about 69 generations, counting 28 years to a generation, and, since the number of ancestors doubles in each generation, it would mean a total of 2^{69} or about 600,000,000,000,000,000,000 individuals in the single generation of our pedigree in A.D. 1. It is obvious that this many people were not alive at that time (there are more people in the world now than ever before, about 2 billion) or, in other words, that the same individuals occurred many times in that and other generations of our pedigree. Your pedigree and mine would probably also show many duplications.

In the sense here used, therefore, "related" animals are those with one or more common ancestors within the first four to six generations and, therefore, with probably more than the average number of genes in common. When two such animals are mated, we call this inbreeding. Diverse opinions are held regarding the practice of inbreeding. Speaking generally, it is in bad repute, because it is believed to result in a more or less degenerate offspring. There can be no doubt, however, that many cases of improvement have also resulted from its use.

In the human family inbreeding is generally frowned upon and proscribed. Many instances of both good and bad results from inbreeding in our species can be cited. In general, however, it is probably a good thing that we do not allow inbreeding in our own species for the reason that our species is the only one which goes out of its way to save its bad genes. In spite of all our efforts to root out bad genes in our livestock, many still persist and make their presence known following inbreeding. In addition, we can dispose of the bad results of inbreeding in our livestock, but not in our own species. So our laws against close matings in our species are justified, but it is unfortunate that this idea is so generally carried over into our thinking about livestock breeding and thus limits the use of inbreeding, one of the most valuable tools in the livestock breeder's kit.

Inbreeding is technically divided into two categories, *viz.*, closebreeding and linebreeding. Closebreeding is the mating of a full brother to sister, of sire to his daughter or dam to her son. These types of matings give the greatest concentration of similar "blood," and this concentration appears close up in pedigree. In fact, the concentration is discovered in the second generation back in all the cases listed as examples of closebreeding. Linebreeding is the mating of animals of wider degrees of relationship than those just stipulated for closebreeding, and is generally directed toward keeping the relationship high to some desirable ancestor or ancestors. In outline form, this is as follows:

- Inbreeding
  - Closebreeding
    - Sire to daughter
    - Son to dam
    - Full brother and sister
  - Linebreeding
    - Half brother and sister or matings of animals more distantly related; *e.g.*, cousin matings, etc.

It should perhaps be pointed out that many breeders use the term *inbreeding* to refer to "close" matings and *linebreeding* to refer to wider ones. Nevertheless, two animals which have any close-up (four to six generations) ancestors are related, *i.e.*, more related than average animals of the breed, and if we mate such animals we are practicing some degree of inbreeding. In this chapter *inbreeding* means either close- or line-breeding, and "close" and "line" are illustrated herewith schematically.

It is said that only 21 Brown Swiss bulls and 129 cows were ever imported to the United States. All the many thousands of Brown Swiss cattle now existing in this country must trace back to these, so that any two Brown Swiss picked at random today quite probably would be found to have some common ancestors if their pedigrees were traced back far enough. Likewise only 6,000 or 7,000 Holsteins were brought to the United States, and the millions of Holsteins now trace back to them and are, therefore, related. So when we say that outbreeding is the mating of unrelated animals and inbreeding the mating of related animals, we are using these terms in the special, limited time sense of four to six generations back. Since there have been, especially in the formative and early stages, particularly favored animals or families in all breeds, it is probable that the animals in any breed are inbred to a small extent.[1]

For example, in a study of Holstein-Friesians born in 1909 these were found to be related to each other about 2.6 per cent relative to the foundation stock of about 1883. If a present-day Holstein-Friesian is related 40 percent to another, both pedigrees being traced back only to 1909, we are not apt to be seriously in error if we assume that the relationship found if both were traced back to 1883 would be about 41.6 per cent (40 per cent plus 2.6 per cent of the remaining 60 per cent). In other words, 40 per cent relative to 1909 is about the same as 41.6 per cent relative to 1883 in this breed.

Two animals that have any close-up ancestors in common are related, and if we mate such animals, we are practicing some degree of inbreeding.

What inbreeding does genetically is to sort the original heterozygous genes out into homozygous form. If we started with organisms that were *Aa Bb* and practiced inbreeding, we could by testing and selection

[1] LUSH, J. L., "Animal Breeding Plans," Collegiate Press, Inc. of Iowa State College, Ames, Iowa, 1945.

sort out strains that were *AA BB*, *AA bb*, *aa BB* or *aa bb*. Neither outbreeding nor inbreeding in themselves change gene frequencies—selection being the only effective tool for doing the latter. Inbreeding separates heterozygous material out into homozygous lines and in this way increases variability.

If we start with a population that is all *Aa* and inbreed it, we get *AA*, 2 *Aa*, and *aa* in the F_1. As the inbreeding progresses, the proportion of *A* and *a* genes, without selection, will remain 50–50. When a line becomes *AA* × *AA* or *aa* × *aa*, it remains there, barring mutation. The *AA* × *Aa*, *AA* × *aa*, *Aa* × *Aa*, and *Aa* × *aa* lines shift about but gradually get into the pure *AA* or *aa* form. In a small line with brother-sister matings about one-fifth of genes which are heterozygous become homozygous in the next generation so that ultimately the population becomes practically all *AA* or *aa*.

You { A { C, D ; B { E, F }

Your father A { C, D }

FIG. 139.—Schematic pedigrees to show father and son relationship (direct).

Relationships.—There are two ways in which animals may be related, *viz.*, directly and/or collaterally. You are directly related to your father, for you are his offspring, and your pedigrees would show many duplications, as indicated in Fig. 139.

Being related to your father means genetically that you and he have more genes in common than do unrelated members of *Homo sapiens*. This is because you both have some common close ancestors. Your father got certain genes from C and D (Fig. 139). You also got some genes from C and D through your father A. One-half of your genes are identical with those your father had, except for a slight discrepancy due to the probable inequality in genes between the X and the Y chromosome if you are a male, and you are therefore related to your father by 50 per cent. Organisms that have common ancestors are related, related organisms probably have more identical genes than nonrelated organisms of the species, and, if related animals are mated, they may both pass duplicate genes to their offspring. In other words, inbreeding has a tendency to make animals more homozygous.

The other type of relationship is called collateral. You and your cousin are collateral relatives because you have some ancestors in common. This is illustrated in Fig. 140.

You and your cousin probably have some identical genes that came to each of you from your common grandparents, C and D. You got yours

through your father, A, your cousin got his through his father, Z (your father's brother or your uncle). The common grandfather, C, might have had a pair of genes *MM* and the common grandmother *mm*. Both your father and your uncle would then have been *Mm*. Whether you and your cousin both got gene *M* or both got gene *m*, or you got *M* and your cousin *m* or vice versa is a matter of chance. With many thousands of genes concerned, however, it is very unlikely that you and your cousin got different members of each pair of heterozygous genes, and these grandparents probably had many homozygous gene pairs, in which cases you and your cousin were sure to get identical genes. In other words, it is very likely that you both received some identical genes from your common grandparents.

You { *A* Your father { *C*, *D*; *B* }

Your cousin { *Z* Your uncle { *C*, *D*; *Y* }

FIG. 140.—Schematic pedigrees to show cousin relationship (collateral).

All cattle probably have some genes in common, but if we mate

Sire X with genes *AA bb Cc Dd Ee FF*

with

Dam Y with genes *AA Bb cc Dd EE ff*

we can have

Kinds of full sisters	$1 \times 2 \times 2 \times 3 \times 2 \times 1 = 24$
Kinds of paternal half sisters	$2 \times 2 \times 3 \times 3 \times 3 \times 2 = 216$
Kinds in the breed	$3 \times 3 \times 3 \times 3 \times 3 \times 3 = 729$

for the genes, unless closely linked in the same chromosome, can become recombined into all the possible combinations. Genetically, therefore, identity of pedigree, except in the case of identical twins, means only similarity of genes unless the animals have become very homozygous through inbreeding and selection. Most of our animals at present, however, are probably rather heterozygous in their genetic make-up; in other words, they received many different genes from each of their parents, a few similar ones.

The two following animals X and Y are full brothers.

Animal X might get gene *A* or gene *a* from S, and animal Y might get *A* or *a* from S. Since there is ½ chance that X will get *A* and ½ chance that Y will get *A*, then the chance that both will get *A* is ¼. They might get 100 per cent the same gene (both *A*, ¼ chance; both *a*, ¼ chance); they might get 0 per cent the same gene (one get *A* and the

other a, ¼ chance, or one get a and the other A, ¼ chance). Therefore, on the average, there is a 50 per cent (½) chance that they will both get the same gene from S. Since the same is true as to genes from the dam D, then X and Y have on the average ½ × ½, or ¼, of their genes as duplicates from S and ½ × ½, or ¼, of their genes as duplicates from D, which means that, on the average, ½ of the genes in X and Y are identical, and they are, therefore, related by 50 per cent, although they have 100 per cent the same "blood." X and Y are full brothers but are only 50 per cent related because of the sampling nature of inheri-

$$X\begin{cases}\text{S } (Aa) \text{ 1 pair of genes} \\ \text{D}\end{cases} \qquad Y\begin{cases}\text{S } (Aa) \\ \text{D}\end{cases}$$

FIG. 141.—Schematic pedigrees of two full brothers.

tance, the fact that a parent passes along only a sample half of its total genetic material to any offspring.

The formula for relationship between X and Y is, therefore,

$$R_{xy} = \text{summation of } [(1/2)^{n+n^1}]$$

The fraction ½ stands for the halving or sampling process of inheritance in each generation, n stands for the number of times this halving or sampling has gone on between S and X, and n^1 stands for the number of times the halving process has gone on between S and Y. Therefore,

for S,	$R = 1/2^{1+1}$ or $1/2^2$ or	25%
and for D,	$R = 1/2^{1+1}$ or $1/2^2$ or	25%
and the summation is R_{xy} =		50%

$$A\begin{cases}B\begin{cases}D\\E\end{cases}\\C\begin{cases}F\\G\end{cases}\end{cases} \qquad X\begin{cases}Y\begin{cases}D\\W\end{cases}\\S\begin{cases}M\\N\end{cases}\end{cases}$$

FIG. 142.—Schematic pedigree of half first cousins.

In a similar fashion it can be shown that in half brothers or sisters ¼ of the genes, on the average, will be identical, and these animals are therefore related by 25 per cent. Similarly, half first cousins, as illustrated in Fig. 142, will have $1/16$ of their genes identical and will, therefore, be related by 6.25 per cent.

In all cases of relationship, we simply apply the formula R_{xy} = summation of all lines of inheritance reaching the related animals from all the common ancestors that they have $[(1/2)^{n+n^1}]$. For the father-son relationship (Fig. 139) we would have $R_{\text{you-your father}} = 1/2^{1+0} = 1/2 = 50\%$, for there is one generation between you and your father, or, in other words, the genetic material has been halved once in getting from your

father to you, and there is no generation between your father and himself. Likewise, in Fig. 142 the relationship between A and X is

$$R_{ax} = \tfrac{1}{2}^{2+2} = \tfrac{1}{2}^{4} = \tfrac{1}{16} = 6.25\%$$

The figure 6.25 per cent means that A and X probably have $\frac{1}{16}$, or 6.25 per cent, more identical genes than unrelated animals of their species and breed.

In the following two pedigrees (Fig. 143) of double first cousins we have still 100 per cent the same "blood"; *i.e.*, both A and B get all their

$$A\begin{cases} C\begin{cases} M \\ N \end{cases} \\ D\begin{cases} O \\ P \end{cases} \end{cases} \qquad B\begin{cases} E\begin{cases} M \\ N \end{cases} \\ F\begin{cases} O \\ P \end{cases} \end{cases}$$

FIG. 143.—Schematic pedigree showing 25 per cent relationship.

blood from M, N, O and P but the sampling process has gone through one more generation than is the case with full brothers so A and B (Fig. 143) are only 25 per cent related.

Applying the relationship formula to A and B we have for M $R = \frac{1}{2}^{2+2}$ and the same for N, O and P so that the summation for all four is $4\frac{1}{2}^{4}$ or 25 per cent.

The term "blood" is being put into quotation marks, because, although it is the usual way the breeder expresses the idea of inheritance, actually,

$$D\begin{cases} E\begin{cases} B \\ C \end{cases} \\ F\begin{cases} B \\ H \end{cases} \end{cases} \qquad E\begin{cases} B \\ C \end{cases}$$

FIG. 144.—Simultaneous direct and collateral relationship.

of course, blood as such does not function in inheritance, this mechanism being provided in the germ cells with their chromosomes and genes. Each embryo produces its own blood, and the only way any animal can get any blood from another, even its own mother, is by means of a blood transfusion. Used in this sense, the term "blood" means inheritance, or chromosomes and genes.

We might, of course, have both direct and collateral relationship at the same time, as illustrated in Fig. 144, in which D and E are related both directly and collaterally, for E is an ancestor (sire) of D (direct), and B is an ancestor of D (through F) and E (collateral). The direct relationship of D and E is expressed by

$$\tfrac{1}{2}^{1+0} = \tfrac{1}{2} = 50\ \%$$

and the collateral relationship by

$$\tfrac{1}{2}^{2+1} = \tfrac{1}{2}^{3} = \underline{12.5\%}$$

Summating, we have

$$R_{DE} = \qquad 62.5\%$$

That is, since E is the sire of D, then D got half of his genes from E and is related to E by 50 per cent. In addition, D and E are related through B, which is the sire of E and also the maternal grandsire of D. What we are asking is how many of the genes that E has are also likely to be found in D, and the answer is 62.5 per cent. If an animal that is a

- Name, N.J.E.S. Mutual Ormsby Jewel Alice No. 654594 Born Dec. 1, 1931
  - Newmont Mutual Ormsby Lad, 493889
    - Ormsby Sensation 45th, 442551
      - Ormsby Sensation, 274343
      - Shady Maple King Pontiac Hockster, 219580
    - Newmont Mutual Scotia, 575310
      - Sir Mutual Scotia, 170631
      - Isa Scotia Beets, 315248
  - Newmont Ormsby Jewel Alice, 1239022
    - Ormsby Sensation 45th, 442551
      - Ormsby Sensation, 274343
      - Shady Maple King Pontiac Hockster, 219580
    - Newmont Ormsby Jewel, 1094461
      - Ormsby Sensation 45th, 442551
      - Clothilde Maid Ormsby Bess

FIG. 145.—Holstein pedigree showing collateral relationship.

common ancestor of two related animals is itself inbred and, therefore, more homozygous, a correction for this fact must be made in the formula for relationship; and likewise, if the animal itself is more inbred than the ancestor, a correction must be made. These corrections will be indicated after we have discussed the coefficient of inbreeding.

Figure 145 shows the pedigree of the Holstein bull N.J.E.S. Mutual Ormsby Jewel Alice. This bull carries 62.5 per cent of the "blood" of Ormsby Sensation 45th getting 25 per cent from each of the latter bull's appearances in the second generation of the pedigree and 12.5 per cent from his appearance in the third generation. Since the amount of Ormsby Sensation 45th "blood" in the bull N.J.E.S. Mutual Ormsby Jewel Alice is the average of that found in his parents, we could find the amount in N.J.E.S. Mutual Ormsby Jewel Alice by averaging the amounts in Newmont Mutual Ormsby Lad and Newmont Ormsby Jewel

Alice. The former has 50 per cent of Ormsby Sensation 45th "blood" and the latter 75 per cent, the average of the total of the two parents being 62.5 per cent as noted above. N.J.E.S. Mutual Ormsby Jewel Alice is 62.5 per cent; Newmont Mutual Ormsby Lad, 50 per cent; and Newmont Ormsby Jewel Alice, 75 per cent related to Ormsby Sensation 45th.

Since the sire and dam of N.J.E.S. Mutual Ormsby Jewel Alice are collaterally related, *i.e.*, have one or more common ancestors, this bull is inbred. He is likely to have gotten identical genes from Ormsby Sensation 45th through three different lines, *viz.*, through his sire, his dam, and his maternal granddam. To find the relationship between the sire and dam, we must brace all these lines and count the generations involved according to our formula $R_{xy} = \Sigma^*[(\frac{1}{2})^{n+n1}]$

From sire to Ormsby Sensation 45th = 1
From dam to Ormsby Sensation 45th = 1 $\therefore \frac{1}{2}^{1+1} = \frac{1}{2}^2 = 25.0\%$
From sire to Ormsby Sensation 45th = 1
From dam through maternal granddam to Ormsby Sensation 45th = 2 $\therefore \frac{1}{2}^{1+2} = \frac{1}{2}^3 = 12.5\%$

37.5%

That is, Newmont Mutual Ormsby Lad and Newmont Ormsby Jewel Alice are 37.5 per cent related (small correction needed for inbreeding involved).

A simpler way of finding this relationship, since these animals are collaterally related through only one common ancestor (Ormsby Sensation 45th), would have been to multiply the percentage of Ormsby Sensation 45th "blood" in each (50 × 75 = 37.5). This latter method becomes complicated, however, where there is more than one common ancestor, especially if these are related.

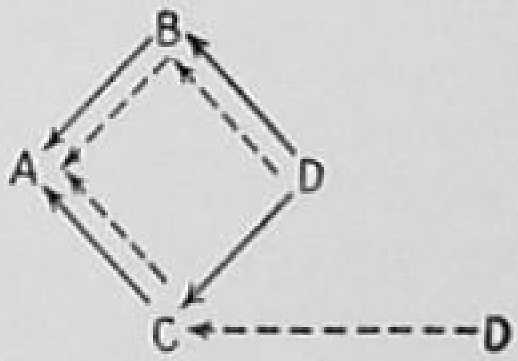


FIG. 146.—Simplified pedigree of Fig. 145.

It may help to simplify matters by writing the pedigree of N.J.E.S. Mutual Ormsby Jewel Alice in a little different form and using letters of the alphabet instead of the actual names. This is done in Fig. 146.

The solid lines from D (Ormsby Sensation 45th) to B and C indicate that both B and C are by D, and that some identical genes may have reached A from D through these two different paths. The same possibility holds for some other identical genes reaching A from D through the paths indicated by the broken lines.

* Greek letter sigma is used for summation.

Direct relationship is what most breeders refer to as *percentage of blood.* They say an animal gets 50 per cent of its "blood" from its sire, 50 per cent from its dam, 25 per cent from each grandparent, 12.5 per cent from each great-grandparent, etc., as illustrated in Fig. 147, together with the figures of chromosomes below using cattle with 60 chromosomes as the example.

Each parent in Fig. 147 is shown as having contributed 30 chromosomes to animal A. These 30 chromosomes were a random sample half of the 60 chromosomes that each of these parents had. The figure shows 15 of them to have come from each grandsire and granddam. This may or may not have been true in any individual case. It would be

Animal A 100% (60)	Sire 50% (30)	Grandsire 25% (15)	Great grandsire 12.5% (7 or 8)	Great great grandsire 6.25% (3 or 4)
			Great granddam	
		Granddam 25% (15)		
	Dam 50% (30)	Grandsire 25% (15)		
		Granddam 25% (15)		
Total blood each generation................	100%	100%	100%	100%
Total chromosomes each generation..........	(60)	(60)	(60)	(60)

FIG. 147.—Showing most probable distribution of "blood" and chromosomes in a cattle pedigree.

possible for the 30 chromosomes that the sire passed on to animal A to have all come from the sire's sire (or from the sire's dam), thus in genetic terms actually terminating one line of the pedigree at that point. It will be noted that there are 60 chromosomes in each generation of the pedigree. In animal A they are found in their entirety. In the parental generation, they are divided between two individuals, the sire and dam. In the grandparental generation, they are divided among four individuals, etc. This illustrates why it is generally not important to trace or consider pedigrees for more than three or four generations, and also why it is unnecessary to pay any particular attention to an outstandingly good or poor individual that occurs farther back than the fourth or fifth generation.

As far as direct relationships are concerned, "percentage of blood" and degree of relationship are seen to be the same thing. It is a mistake,

however, to try to use "percentage of common blood," as a measure of relationship between animals related collaterally. Figure 141 showed two full brothers X and Y to have 100 per cent the same "blood" and to be related by 50 per cent. Figure 143, on the other hand, showed the two double first cousins A and B also to have 100 per cent the same "blood" but to be related by only 25 per cent because of the additional intervening generation.

Coefficient of Inbreeding.—As indicated earlier, inbreeding results whenever related animals are mated. We have already seen that full brothers and sisters are related by 50 per cent; *i.e.*, ½ of their genes are

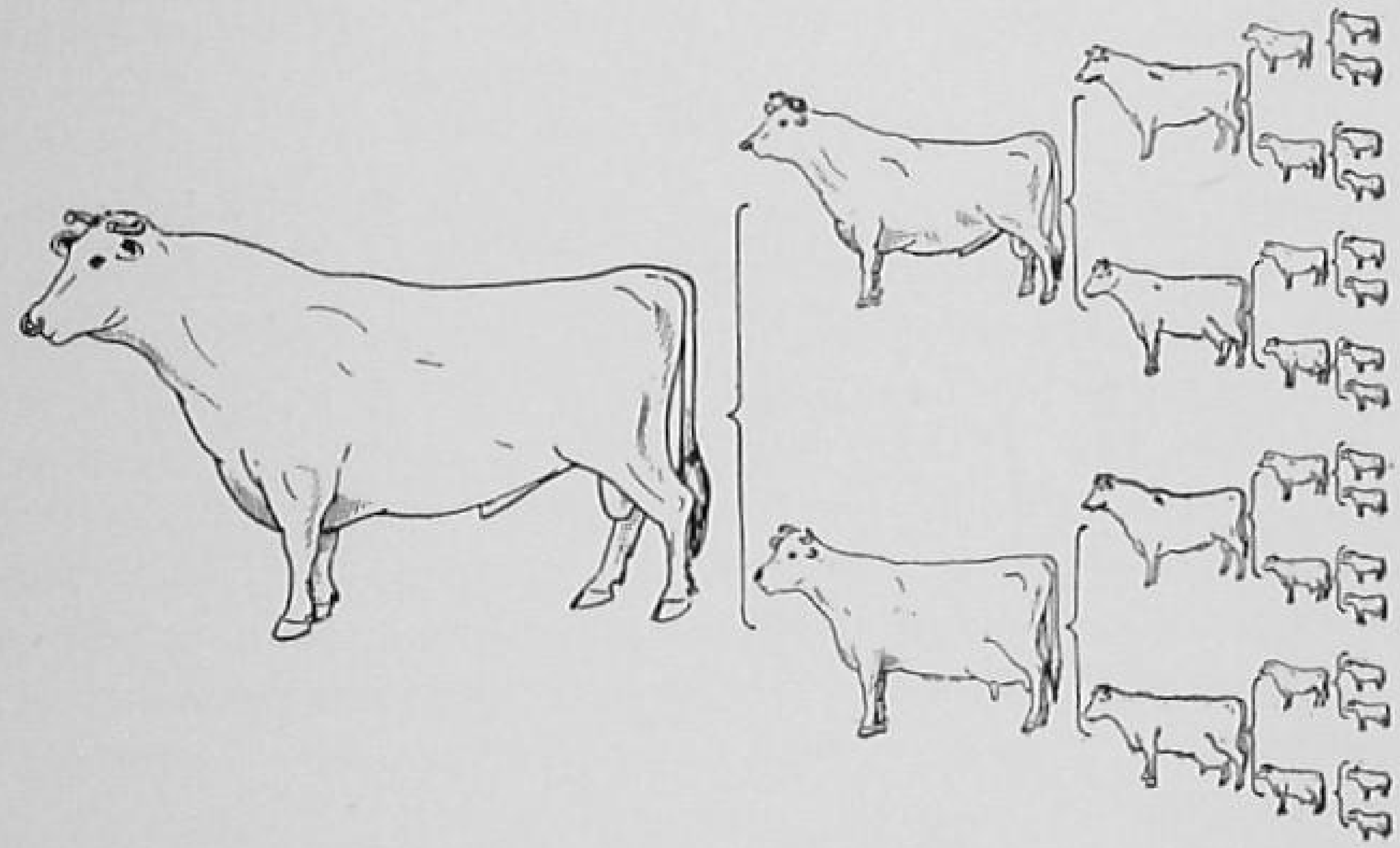


FIG. 148.—Pictorial pedigree showing relative size of ancestors in terms of their contribution according to Galton's law.

probably duplicates (¼ from each parent). Now, if a full brother and sister are mated, we produce a new generation that is once further removed from the common ancestors. Since each such removal halves the genetic material, we can simply multiply the relationships between the full brother and sister (50 per cent) by ½ and thus arrive at the coefficient of inbreeding for the new individual.

In other words, to find the coefficient of inbreeding of any animal, we can first find the coefficient of relationship between its sire and dam and then divide this amount by 2. Figure 149 represents such a mating.

Another way to do this is to count the number of times the genetic material has been halved in getting to the parents of the inbred animal from the common ancestor (or ancestors) and then adding 1 to the exponent of ½ to take care of the halving in getting from the sire and dam to the inbred animal in question. This gives us the formula for inbreed-

ing suggested by Wright[1] as

$$F_x = \Sigma[(\tfrac{1}{2})^{n+n^1+1}]^*$$

This formula measures the reduction of heterozygosity in relation to the foundation stock in the most remote generation of the pedigree being considered. Figure 150 shows a half brother-sister mating, B and C being 25 per cent related, because there is one generation from B back to the common ancestor D and also one generation from C back to D.

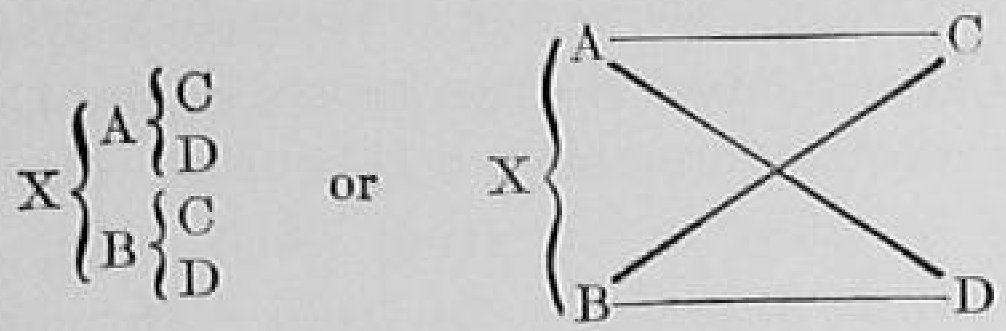


FIG. 149.—Full brother-sister mating.

The only common ancestor here is D. From the sire back to the common ancestor is 1 (n in formula); from the dam back to the common ancestor is 1 (n^1 in formula); and the 1 that must be added to take care of the halving in getting from B and C to X gives us a total of 3 as the exponent of $\frac{1}{2}$, and $\frac{1}{2}^3 = \frac{1}{8}$, or 12.5 per cent as the inbreeding coefficient of X. This figure 12.5 per cent simply means that this system of mating has reduced the heterozygosity (or increased the homozygosity) by that amount over what it was in the generation containing D, E, and F. If the animals D, E, and F were 50 per cent homozygous and 50 per

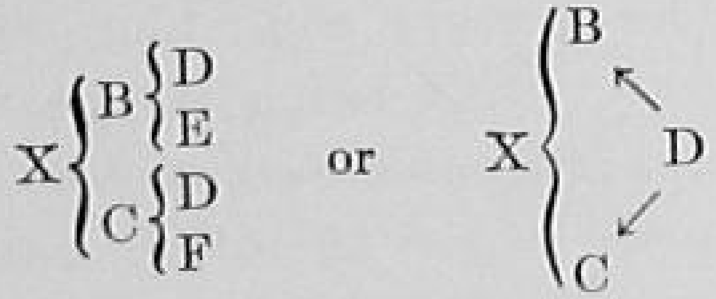


FIG. 150.—Schematic half brother-sister mating.

cent heterozygous, then animal X is 12.5 per cent less heterozygous or $50\% \times 12.5 = 6.25\%$ less heterozygous than they were, or only 43.75 per cent heterozygous. Looked at the other way, X is now 56.25 per cent homozygous.

If a common ancestor is himself or herself inbred, this will, of course, make a difference in the likelihood of its inbred descendant getting identical genes from each of its parents. Being inbred means that the common ancestor (A) is homozygous for more pairs of genes than is an outbred one. In other words, two offspring of such an inbred animal have less chance of receiving different genes from this ancestor and

[1] WRIGHT, S., Coefficients of Inbreeding, *Amer. Nat.*, **56**:330–338, 1922.

* Complete formula will be found below.

likewise more chance of receiving identical genes. This fact is provided for by changing the formula for inbreeding from

$$F_x = \Sigma[(\tfrac{1}{2})^{n+n+1}] \quad \text{to} \quad F_x = \Sigma[(\tfrac{1}{2})^{n+n'+1}.\ (1 + F_A)]$$

In other words, if $\Sigma[(\frac{1}{2})^{n+n'+1}]$ was found in a given case to be 25 per cent, but the common ancestor was himself or herself inbred by 12.5 per cent, then we would have to multiply 25 per cent by 1.125 per cent, making the final inbreeding 28.125 per cent.

A case of this sort is shown in Fig. 151 with X 26.56 per cent inbred.

It is obvious in Fig. 151 that X is an inbred animal, for it resulted from the mating of full brother and sister B and C. In other words, X is more homozygous because it received some identical genes from D through its sire and dam and also some from E through its sire and dam. But D, one of the common ancestors, is also seen to have been an inbred

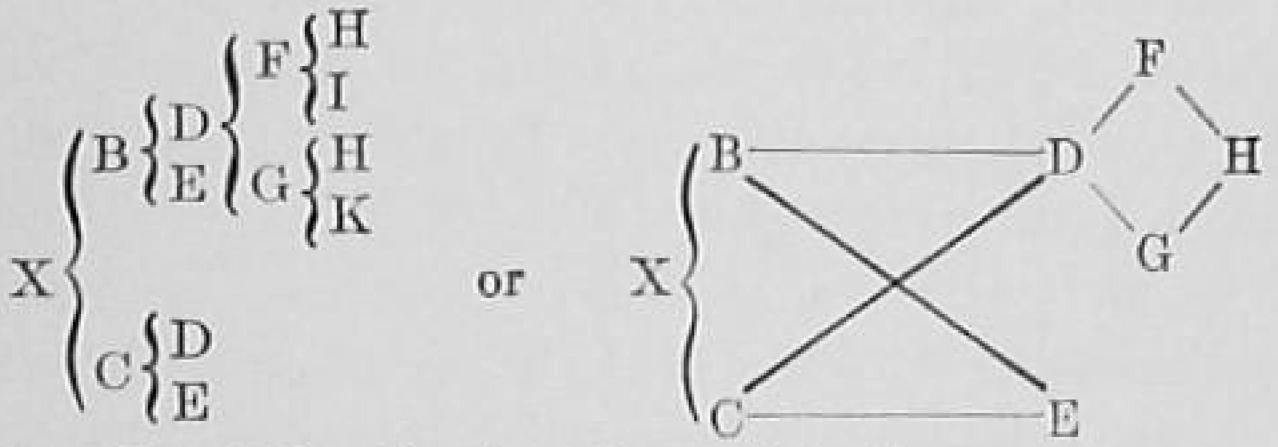


Fig. 151.—Inbreeding involving an inbred common ancestor.

animal; in other words, D had more homozygous sets of genes than an outbred animal because he received some identical genes from H through both his sire and his dam. This being the case, D would be expected to have fewer sets of heterozygous genes, one member of which would be passed to X through its sire B and the other member of which would be passed to X through its dam C. If D were not inbred, he might be homozygous for certain genes, but, if he is inbred, he is undoubtedly homozygous for more sets of genes. Since the coefficient of inbreeding measures directly the probable increase in homozygosity, the inbreeding of any animal must be multiplied by 1 plus the percentage inbreeding of any common ancestors that are themselves inbred, in other words, must be increased by the added amount of homozygosity due to the increased homozygosity of its inbred common ancestors. We cannot, of course, know the actual amount of homo- or heterozygosity for any animal. The coefficient of inbreeding simply accounts for the added homozygosity due to the opportunity an animal has of getting identical genes from any ancestors that are common to its sire and dam.

Figure 152 shows the pedigree of an animal that has some repeats in its pedigree but is not an inbred animal because it has no common

ancestor on both sides of its pedigree; in other words, its sire and dam are not related.

It is true that animal B is inbred, since it resulted from a full brother-sister mating. Animal B is 25 per cent inbred, 25 per cent more homozygous than its immediate ancestors were, but B transmits to A only one-half of its genetic material, one member of each pair of genes that it has and there is nothing in the pedigree of A to lead us to suspect that B and C will pass identical genes to A. Animal A, therefore, is not inbred. By the same token, we might mate a highly inbred Holstein bull to a highly inbred Guernsey cow. The resulting offspring would, of course, not be inbred although both of its parents were, but crossbred. The inbred Holstein and Guernsey would not be likely to pass identical genes to their offspring, although since they both belong to the species cattle,

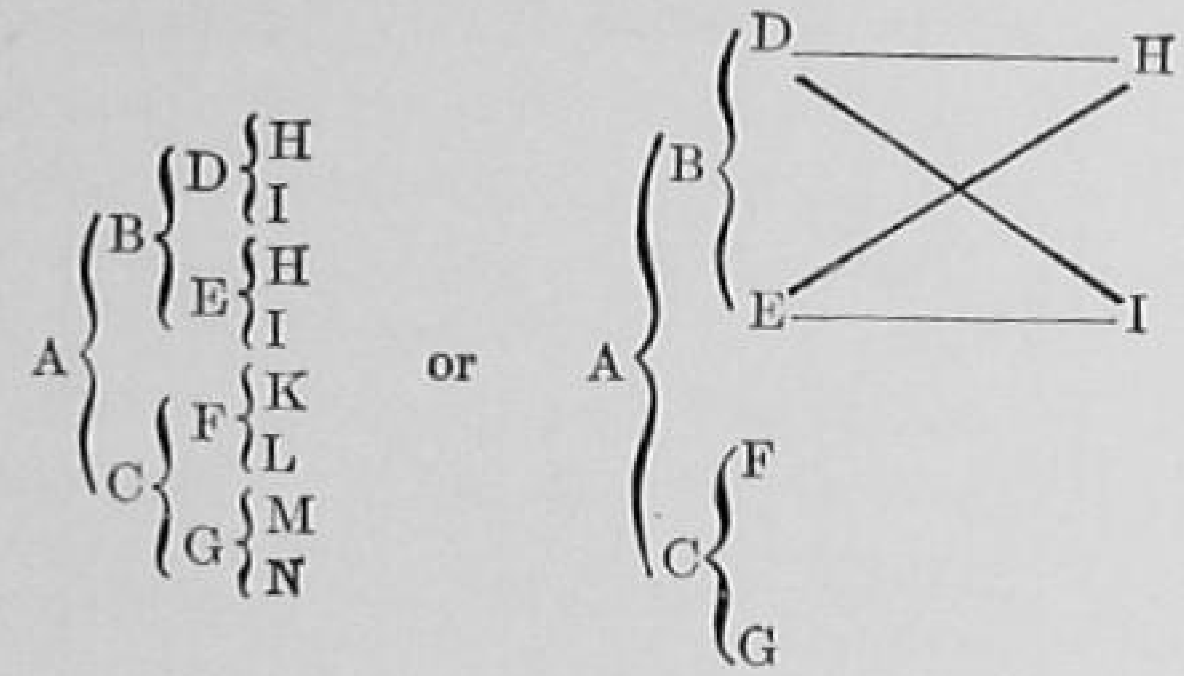


FIG. 152.—Pedigree of an outbred animal.

they probably do have some genes in common and might, therefore, pass some identical genes to their offspring.[1]

A decline in heterozygosity should result automatically under continued self-fertilization or closebreeding. Thus an individual heterozygous for a single factor pair *Aa* will produce, if selfed, offspring of which one-fourth are *AA*, one-half *Aa*, and one-fourth *aa*. Under continued selfing the homozygous types breed true and are progressively augmented by segregates from the dwindling group of heterozygotes. The proportions of the three groups may be determined by any generation by the formula developed by Mendel:

$$2^n - 1\ AA : 2\ Aa : 2^n - 1\ aa$$

where n is the number of generations of self-fertilization.

Similar formulas have been developed by which it is possible to compute the results of other systems of mating. Thus in brother-sister mating the proportion of homozygosity progressively increases but at a slower rate, 6 generations of

[1] From EAST, E. M., and JONES, D. F., "Inbreeding and Outbreeding," J. B. Lippincott Company, Philadelphia, 1919.

self-fertilization being approximately as effective as 17 generations of brother-sister mating.

This reduction in heterozygosity[1] takes place automatically in all other factor pairs regardless of the number of pairs involved (Fig. 153). Thus continued self-fertilization leads to a decline in heterozygosity for about seven generations, about 99 per cent of homozygosity being attained in the seventh generation. This resembles the actual results of inbreeding, for here there is a decline in size and variability for about seven or eight generations, after which a line becomes essentially stable.

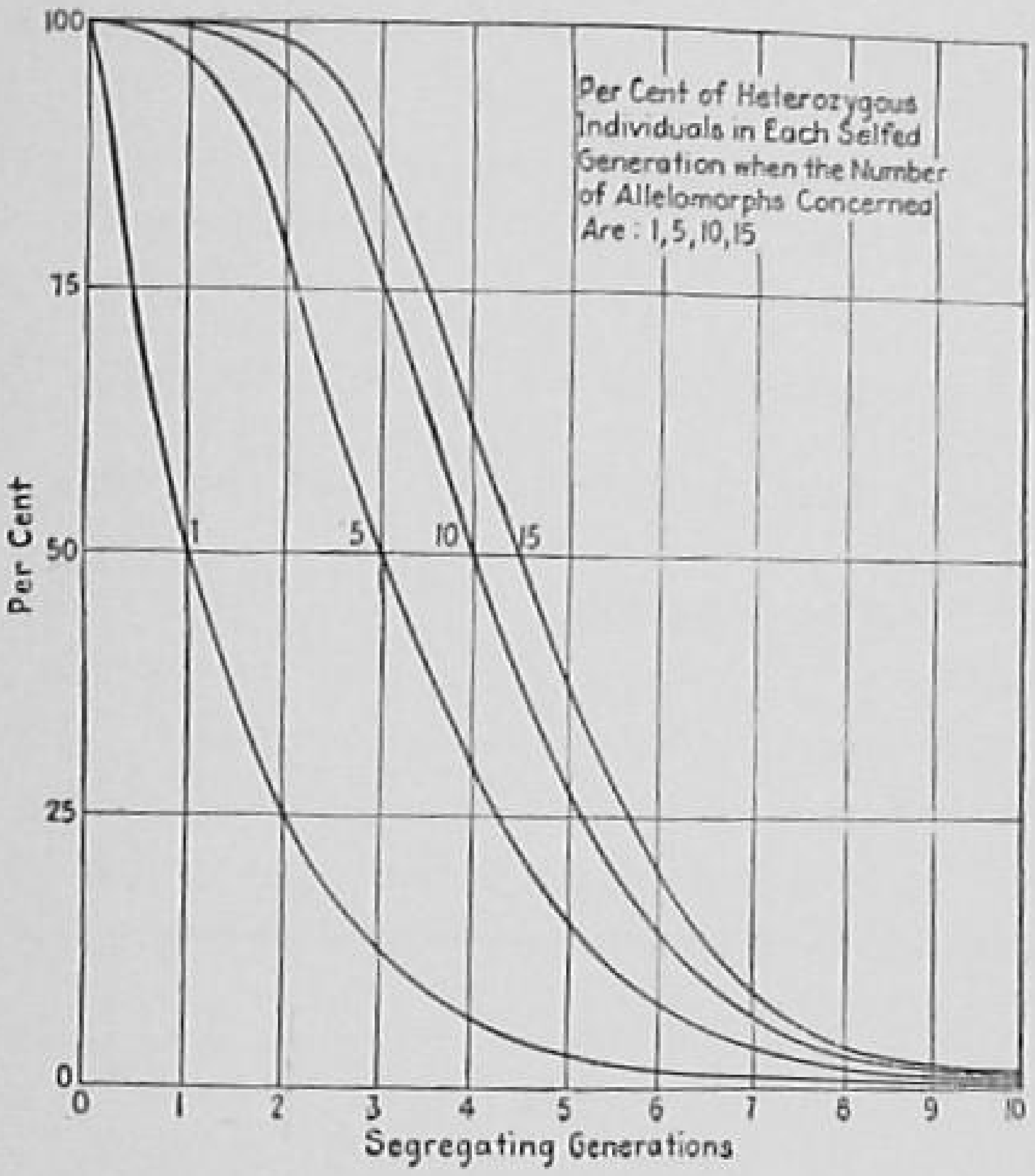


FIG. 153.—Graph showing the reduction in the proportion of heterozygous individuals and of heterozygous factor pairs in successive generations of self-fertilization. (*After East and Jones.*)

All the evidence can best to interpreted, therefore, as indicating that the reduction in size and vigor is related in some way to the attainment of homozygosity and that the mere process of inbreeding, of itself, does not produce this result. The automatic reduction of heterozygosity will occur, of course, only if new mutations in inbred lines are very rare. If the mutation rate is high, this may defer or prevent the attainment of homozygosity.

Coefficient of Relationship.—Because of the fact that inbreeding makes an animal more homozygous, and, therefore, if said animal is a common ancestor of two related animals makes it more likely that he

[1]SINNOTT, E. W., and DUNN, L. C., "Principles of Genetics," 3d ed., McGraw-Hill Book Company, Inc., New York, 1939.

will pass identical genes to both descendants, and also because inbreeding makes a population more variable by producing separate inbred strains, two corrections are needed in the formula for relationship to make it scientifically correct. To take care of the fact that an inbred common ancestor is more likely to pass identical genes to two descendants, because his inbreeding has made him more homozygous, the numerator of the relationship coefficient must have added to it $(1 + F_a)$ as a multiplier, as we have just seen; and to take care of the fact that inbreeding tends to create separate families, a denominator must be supplied in the form of $1 + F_x$, $1 + F_y$ making the complete formula for relationship between animals X and Y.

$$R_{xy} = \frac{\Sigma[(\frac{1}{2})^{n+n1} \cdot (1 + F_a)]}{\sqrt{1 + F_x} \cdot \sqrt{1 + F_y}}$$

In the mating for instance, of a son to his own dam, the relationship between his offspring and his noninbred dam becomes $\frac{75\%}{\sqrt{1 + F_0}}$. In this case the most probable situation is that in half the pairs of genes in the offspring both members will have come from the common ancestor. But in half those cases the two genes will be duplicates of only one gene that the common ancestor had, so that in one-quarter of the pairs of genes the offspring will be homozygous, whereas the common ancestor was heterozygous, although both of the offsprings' genes came from the common ancestor. This is illustrated in Fig. 154.

$$O\begin{cases} S\begin{cases} F \\ D \end{cases} \\ \\ D \end{cases} \qquad R_{OD} = \frac{75}{\sqrt{1 + F_0}} = \frac{75}{\sqrt{1 + 0.25}} = \frac{75}{1.1} = 68.2$$

FIG. 154.—Parent-offspring mating with relationship computed.

The real function of these corrections is to reveal the actual degree in which the genotype of related animals are similar, rather than leave it in terms of the percentage of genes from a common source. In the above parent-offspring mating, it is most likely that 75 per cent of the genes of the offspring O came from its dam and paternal granddam D, but since the offspring is inbred, whereas the parent D was not, then O will have a certain number of homozygous gene pairs that existed as heterozygous pairs in the parent D.

Because there has been so little inbreeding practiced in our farm livestock, the denominator of the complete relationship coefficient seldom becomes very much larger than 1.0 and can, therefore, be dispensed with in general practice.

The final form of the formula for direct or ancestor-descendant relationship becomes

$$R_{za} = \sum \left(\frac{1^n}{2}\right) \sqrt{\frac{1 + F_a}{1 + F_z}}$$

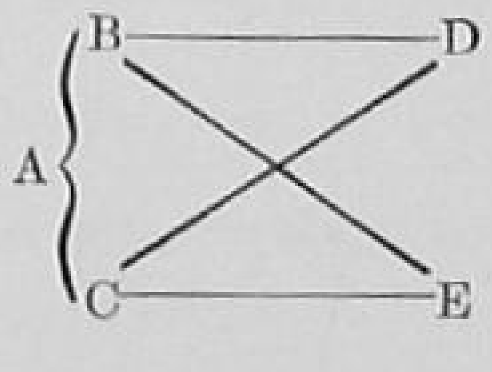
The term under the square-root sign in this formula is necessary owing to the fact that, if the ancestor is more highly inbred (more homozygous) than the descendant, the coefficient of relationship will be larger than the "percentage of blood," and vice versa. In most pedigrees of our farm animals, however, there is not likely to be enough difference in the amount of inbreeding of ancestor and descendant but that the portion of the complete formula under the radical can be dispensed with.

The following table will be found convenient in working out inbreeding coefficients.

Table 33.—Exponential Values of ½

$\frac{1}{2}^2$	= ¼	= 25.0%
$\frac{1}{2}^3$	= ⅛	= 12.5%
$\frac{1}{2}^4$	= 1/16	= 6.25%
$\frac{1}{2}^5$	= 1/32	= 3.125%
$\frac{1}{2}^6$	= 1/64	= 1.5625%
$\frac{1}{2}^7$	= 1/128	= 0.78125%
$\frac{1}{2}^8$	= 1/256	= 0.390625%
$\frac{1}{2}^9$	= 1/512	= 0.1953125%

In the mating of full brother and sister we have seen that the coefficient of inbreeding is 25 per cent.



In the case of continued full brother-sister matings for two generations the inbreeding coefficient would be 37.5 per cent.

It should be observed that we trace back from B, the sire, to D, a common ancestor, then down to D on the dam's side of the pedigree, and then forward to the dam. We do this also for E, another common ancestor in the second generation, and this completes all the ancestors in this generation. Now we move to the third generation where we find the same two animals F and G in each line of the pedigree. When we traced the paths through D a moment ago, we also took care of the F's and G's

in these lines, since the likelihood of animal A getting identical genes from D is taken care of in its entirety when we trace the D paths and is not increased because of the F's and G's behind D. The same thing applies to the E's in the second generation. However, since the presence of F and G behind D on the top side of the pedigree and behind E on the bottom side (and E on the top side and D on the bottom side) does give additional opportunities for A to get identical genes through these paths, these opportunities must be evaluated.

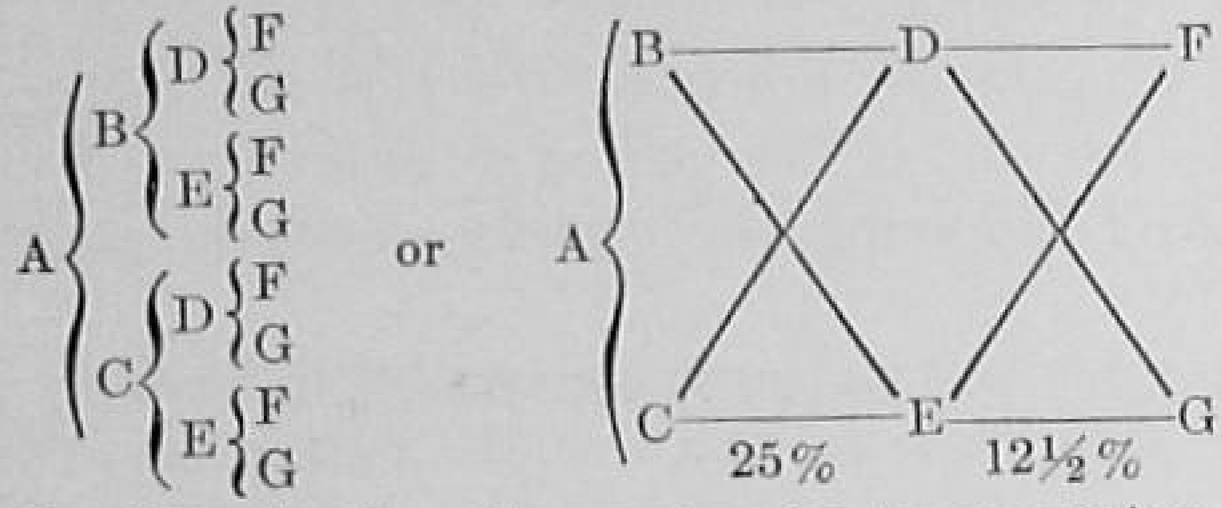


FIG. 155.—Brother-sister matings for two generations.

We have, therefore, in this two-generation full brother-sister mating four common ancestors, D, E, F, and G, and they have the following values.

$$
\begin{aligned}
D &= \tfrac{1}{2}^{1+1+1} &&= \tfrac{1}{2}^{3} &&= 12.5\% \\
E &= \tfrac{1}{2}^{1+1+1} &&= \tfrac{1}{2}^{3} &&= 12.5\% \\
F &= \tfrac{1}{2}^{2+2+1} \times 2 &&= \tfrac{1}{2}^{5} \times 2 &&= 6.25\% \\
G &= \tfrac{1}{2}^{2+2+1} \times 2 &&= \tfrac{1}{2}^{5} \times 2 &&= 6.25\% \\
& && \text{Total} && 37.5\%
\end{aligned}
$$

With three generations of full brother-sister matings, we would have

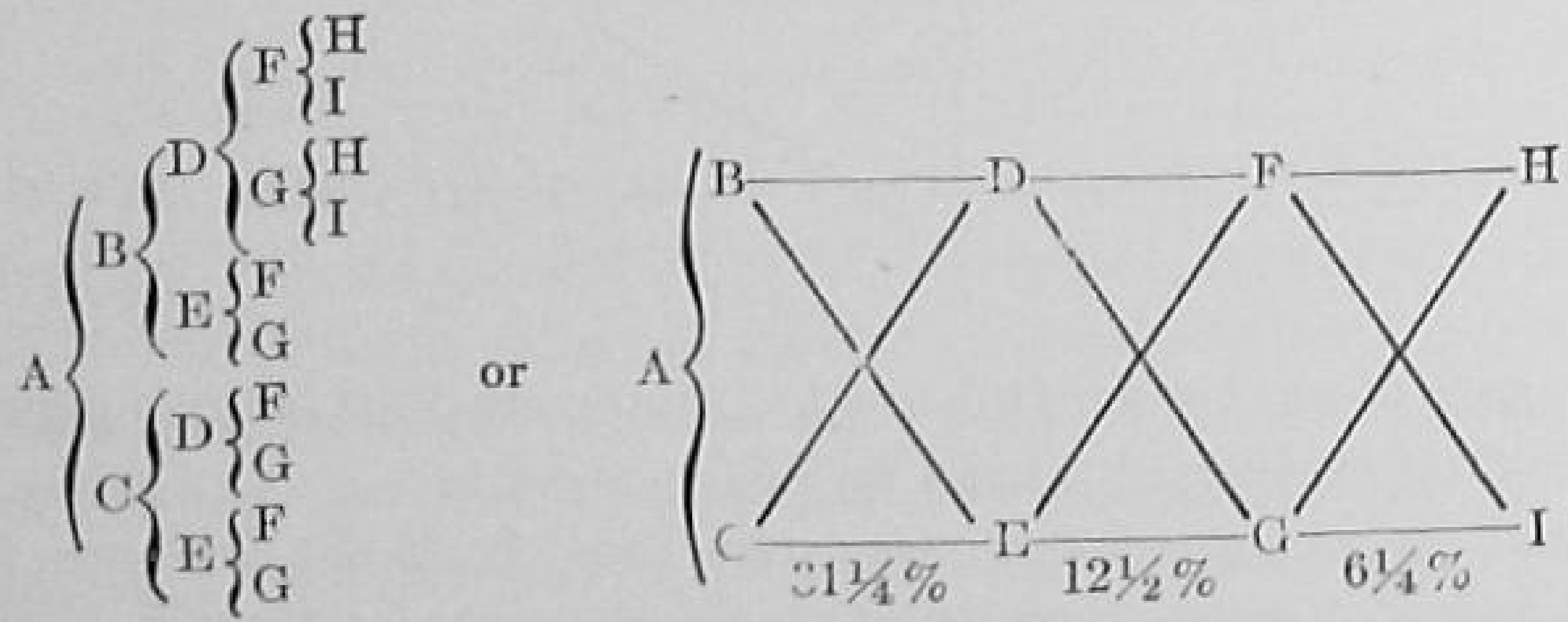


FIG. 156.—Brother-sister matings for three generations.

Here we meet the fact that some of the common ancestors (D and E) are themselves inbred, so that our summation of all the different paths, by means of which A might get identical genes from its common ancestors, is

$$D = \tfrac{1}{2}^3 \times 1.25 = 15.625\%$$
$$E = \tfrac{1}{2}^3 \times 1.25 = 15.625\%$$
$$F = \tfrac{1}{2}^5 \times 2 = 6.250\%$$
$$G = \tfrac{1}{2}^5 \times 2 = 6.250\%$$
$$H = \tfrac{1}{2}^7 \times 4 = 3.125\%$$
$$I = \tfrac{1}{2}^7 \times 4 = 3.125\%$$
$$\text{Total} \quad 50.000\%$$

In Fig. 156 it is evident that the sire B and dam C are connected through two lines involving two generations, through four lines involving four generations, and through eight lines involving six generations. In

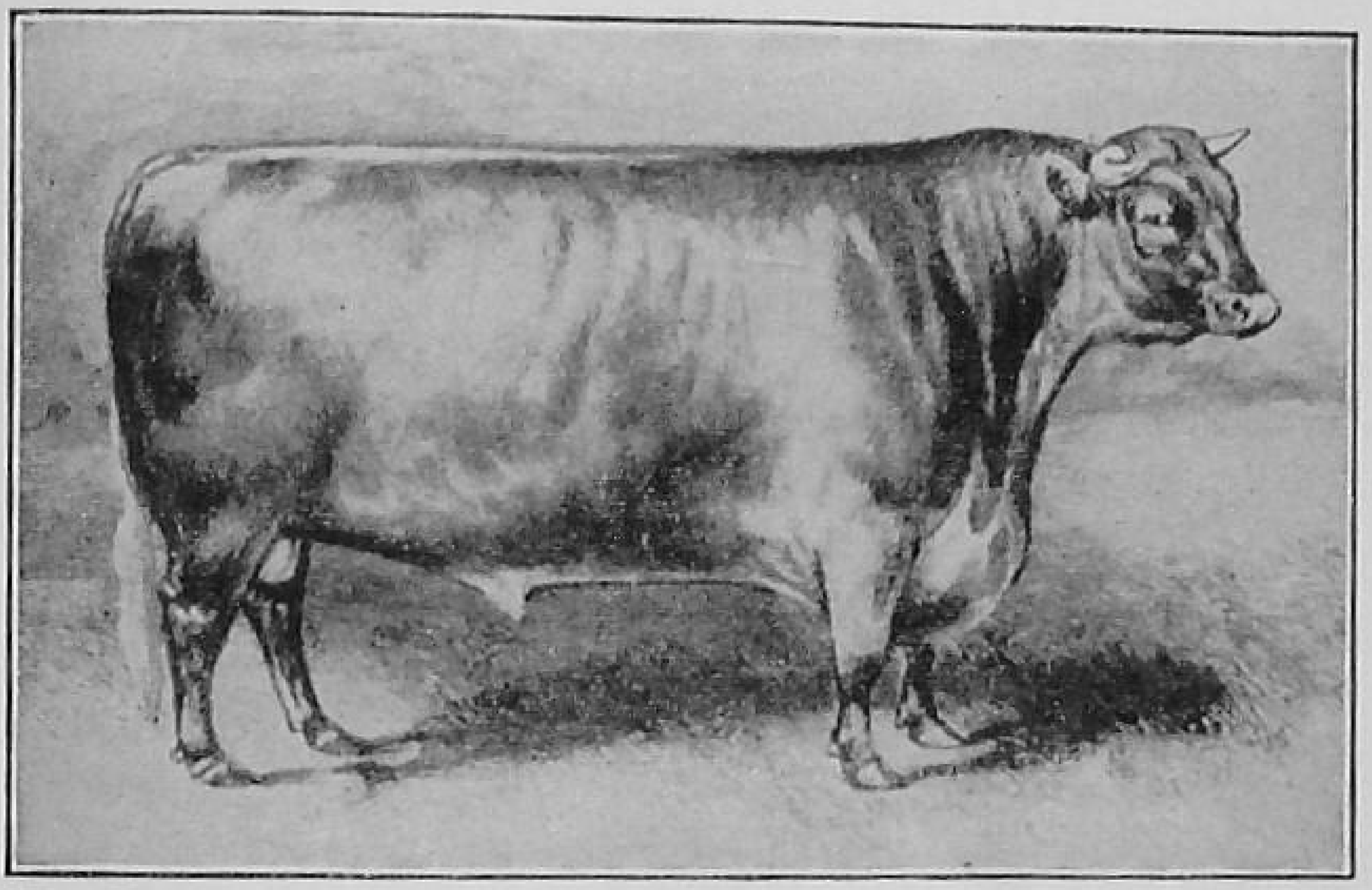


FIG. 157.—Comet (155). The first bull ever sold for $5,000. He was very strongly inbred. (*From Sanders, Shorthorn Cattle, The Breeders Gazette.*)

addition, the parents of the sire and dam have one generation of inbreeding behind them, or 25 per cent. Our formula becomes, therefore,

$$F_x = \Sigma_2[(\tfrac{1}{2})^3 \times 1.25] + 4[(\tfrac{1}{2})^5] + 8[(\tfrac{1}{2})^7] = 50\%$$

This shows that, assuming a 50 per cent heterozygous condition to start with, an individual which is the result of three generations of full brother-sister matings is now 75 per cent homozygous.

In full brother-sister matings one generation gives an inbreeding coefficient of 25 per cent; two generations, 37.5 per cent; three generations, 50 per cent; ten generations, 88.6 per cent. In parent-offspring matings, one generation gives an inbreeding coefficient of 25 per cent; two generations, 37.5 per cent; three generations, 43.8 per cent, approaching 50 per cent as a limit.

- Comet (155) ....
  - Favorite (252)
    - Bolingbroke (86)
      - Foljambe (263)
        - R. Barker's bull (52)
        - Haughton
      - Young Strawberry
        - Dalton Duke (188)
        - Favorite (cow)
    - Phoenix
      - Foljambe (263)
        - R. Barker's bull (52)
        - Haughton
      - Favorite (cow)
        - Alcock's bull (19)
        - ....
  - Young Phoenix
    - Favorite (252)
      - Bolingbroke (86)
        - Foljambe (263)
        - Young Strawberry
      - Phoenix
        - Foljambe (263)
        - Favorite (cow)
    - Phoenix
      - Foljambe (263)
        - R. Barker's bull (52)
        - Haughton
      - Favorite (cow)
        - Alcock's bull (19)
        - ....

FIG. 158.—Pedigree of Shorthorn bull, Comet.

From a practical standpoint, the obvious use of relationship is to assess the probable merit of an untested animal by its relationship to tested ones. If a cow produced 50 lb. of butterfat above the breed average, her daughter 50 per cent related could be expected to produce 25 lb. above breed average. Other more distant relatives could be assessed on their degree of relationship. This is practical within limits but leaves out of account the sire involved and various effects of environment, dominance, and epistasis. We cannot know the complete genotype of any animal and must of necessity consider the phenotype to be a more or less accurate indication of genotype, which it may or may not be.

As will be pointed out later, we are in great need of broadening our basis of selection by considering family as well as individuality. In this, in- or linebreeding to set off separate strains or families and relationship to help measure probable genetic merit should find an ever-increasing usefulness.

Examples of Inbreeding.—Figure 158 gives the pedigree of the famous Shorthorn bull Comet, the first bull ever sold for as much as $5,000.

As will be noted, the bull Favorite was bred back to his own dam Phoenix and their offspring Young Phoenix bred to her sire Favorite. Since Favorite is himself inbred, we shall first compute his coefficient of inbreeding. His sire and dam are related through the bull Foljambe and the cow Favorite, our formula being

$$F_A = \Sigma[(\tfrac{1}{2})^3] + [(\tfrac{1}{2})^4] = 18.75\%$$

As shown in the pedigree, Comet has four common ancestors, *viz.*, Favorite (bull), Phoenix, Foljambe, and Favorite (cow), and our formula becomes

$$\begin{aligned} F_x &= \Sigma[(\tfrac{1}{2})^2 \times 1.1875] + [(\tfrac{1}{2})^3] + [(\tfrac{1}{2}^5)] + [(\tfrac{1}{2}^6)] \\ &= 0.2969 + 0.1250 + 0.0312 + 0.0156 \\ &= 46.87\% \text{ coefficient of inbreeding for Comet} \end{aligned}$$

We can perhaps see this more clearly if we skeletonize the pedigree of Comet and use letters instead of names as in Fig. 159.

It is evident from Fig. 159 that one of the common ancestors, B, is himself inbred and that E, F, and H are also common ancestors.

Figure 160 gives the pedigree of the Jersey bull Sybil's Gamboge. The sire and dam of this bull are more than half brother and sister, the sire is the result of mating a three-quarter brother and sister, and the dam of Sybil's Gamboge traces in all four lines to the bull Champion Flying Fox, for he is the sire of both Gedney Farm Oxford Lad and of Agatha's Flying Fox.

We notice that there are five ancestors in his pedigree (Fig. 160) that are common to both sire and dam, *viz.*, Oxford Majesty, Royal Majesty, Gedney Farm Oxford Lad, Fontaine's Oxford Pride, and Champion Flying Fox, and we also notice that Oxford Majesty, one of the common ancestors, is himself inbred. We have, therefore,

Oxford Majesty. One chain of two generations, together with his own inbreeding coefficient of 12.5 per cent. Contribution $(\frac{1}{2})^3 \times 1.125$.

Royal Majesty. One chain of four generations (the other chain having been accounted for in working with Oxford Majesty). Contribution $(\frac{1}{2})^5$.

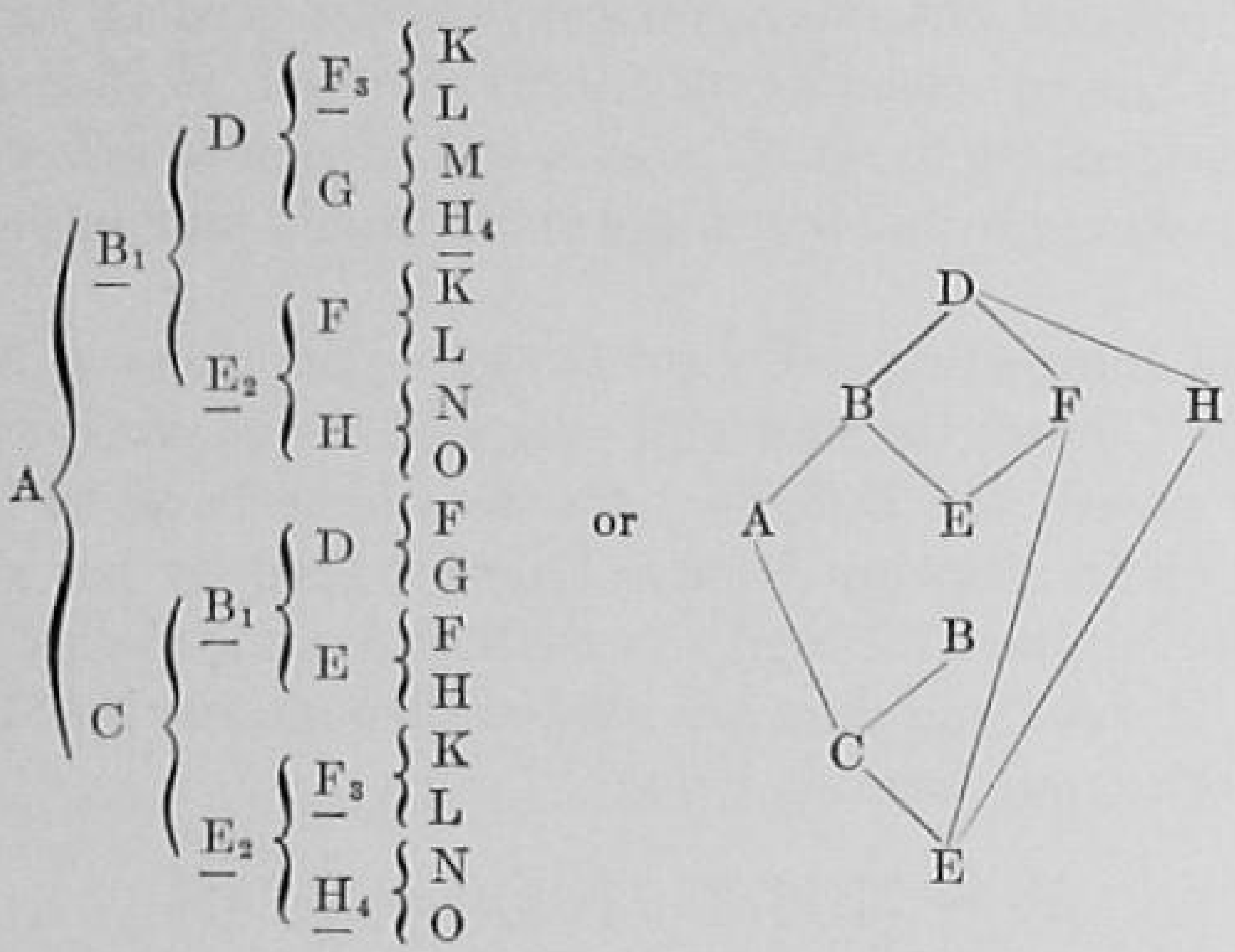


FIG. 159.—Skeletonized pedigree of Comet.

Gedney Farm Oxford Lad. Seven remaining chains of six generations. Contribution $7 \times (\frac{1}{2})^7$.

Fontaine's Oxford Pride. One chain of six generations. Contribution $(\frac{1}{2})^7$.

Champion Flying Fox. Four remaining chains of eight generations. Contribution $4 \times (\frac{1}{2})^9$.

Total. F_x for Sybil's Gamboge = 24.22%.

Role of Inbreeding.—Now that we understand the basic principles underlying inbreeding, it will no longer surprise us that both good and harmful results arise from its use. Inbreeding in itself does not create any new genes, nor for that matter does any system of breeding. All that any system can do is to recombine the genes already present into new combinations. With outbreeding, we tend to keep our livestock heterozygous. With inbreeding, we make them more homozygous. If we have a preponderance of good genes and gene combinations in our stock to start with, inbreeding plus selection will increase the good qualities

Name: Sybil's Gamboge
Registry No.: 174663
Date of Birth: March 16, 1914

Sire: Imp. Gamboge's Royal Majesty 149864	Imp. Oxford Majesty 134090	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
			Oxford Ixia 3rd 8584
		Oxford Lad's Lucy 213913	Gedney Farm Oxford Lad 71238
			Lucy 12th 9236
	Majesty's Pride 2nd 14462	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
			Oxford Ixia 3rd 8584
		Oxford's Fontaine 224580	Gedney Farm Oxford Lad 71238
			Fontaine Oxford Pride 187430
Dam: Gamboge Oxford Sybil 337787	Imp. Oxford Majesty 134090	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
			Oxford Ixia 3rd 8584
		Oxford Lad's Lucy 213913	Gedney Farm Oxford Lad 71238
			Lucy 12th 9236
	Gamboge's Prosperity 252142	Gamboge's Knight 95698	Agatha's Flying Fox 3256
			Fontaine's Oxford Pride 187430
		Oxford's Fawn Lucy 238439	Gedney Farm Oxford Lad 71238
			Cynthia 7927

FIG. 160.—Pedigree of Sybil's Gamboge.

we already have. If we have a preponderance of poor genes and gene combinations to start with, inbreeding will increase the poor qualities we already have.

What inbreeding actually does is to fix characters. These characters may be either good, bad, or indifferent, and whatever they are, inbreeding will not change them in the least. Inbreeding is no more potent than any other system in creating new characters of any sort; in fact, it is less so, for variation is reduced. All that inbreeding does is to take the genes that are present and sort them out into homozygous forms. For instance, if an animal was carrying several genes, or determiners, for characters in the heterozygous form, *i.e.*, one parent after reduction had put in *AbC* and the other one *aBc*, the hybrid would carry *Aa Bb Cc*. If such an

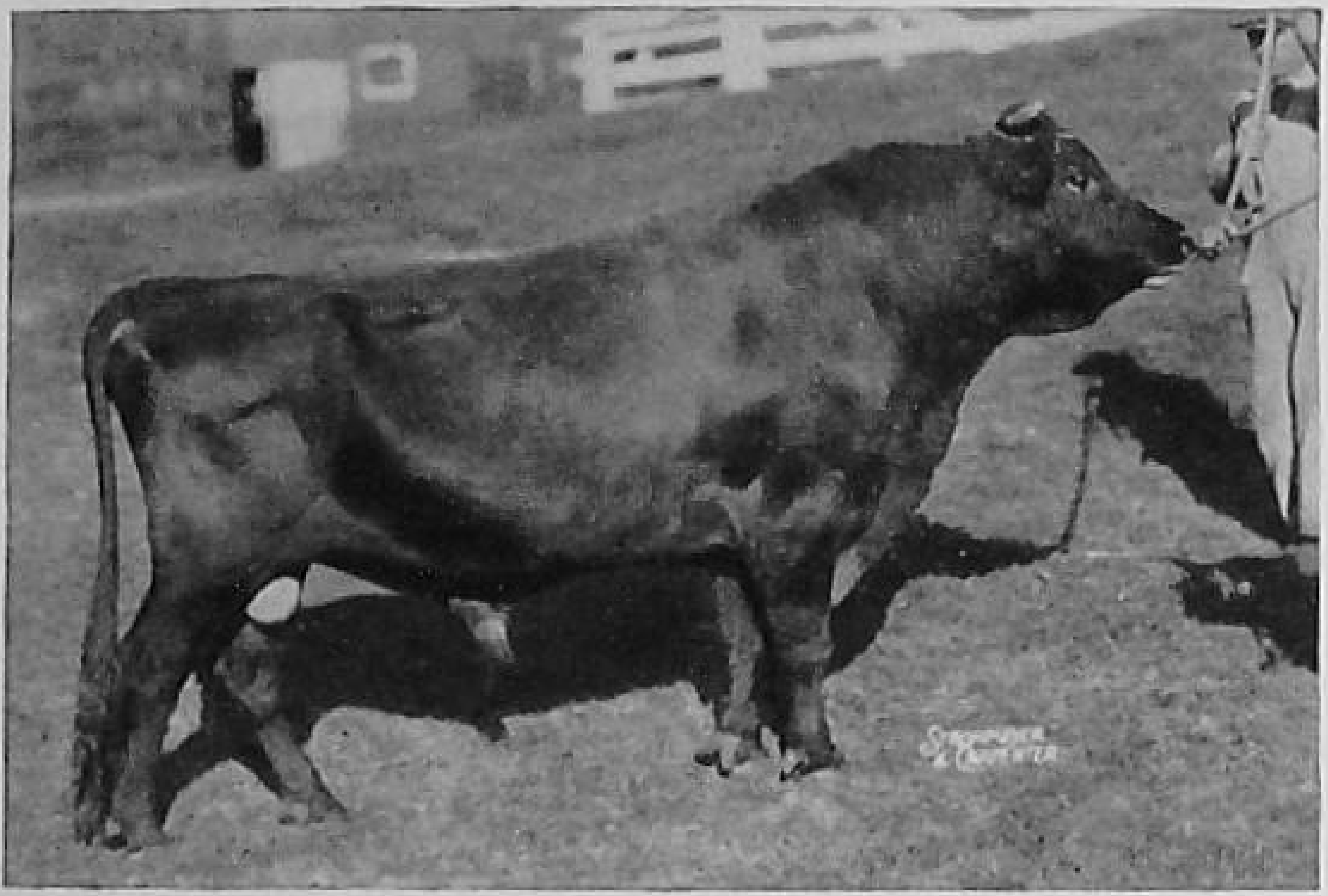


FIG. 161.—Sybil's Gamboge, a strongly inbred Jersey bull.

animal were bred to another animal of similar genetic constitution, the genes would tend to combine in all possible combinations from *AA BB CC* to *aa bb cc*. Then if sufficient numbers were available so that rigid selection could be practiced, the *AA BB CC* type could be selected out. Supposing that in the foregoing, the capital letters stood for desirable characteristics and the small letters for undesirable ones, one can see why inbreeding may give either good or bad results, because *AA BB CC* animals with no recessive, undesirable factors would be a decided improvement over either parent, whereas *aa bb cc* animals would be just the reverse. It will bear repeating that inbreeding is powerless to create either good or bad. It is, however, the very best method of finding out what is present in a strain, for inbreeding will sort out the various genes into a homozygous condition. The desirable animals may then be retained and the undesirable ones discarded.

Animals might be carrying recessive genes for lethal factors, for lack of fertility, for weak constitution, for inefficient production, etc. If we outbreed such animals to good sires, these undesirable recessives are likely to remain hidden and unsuspected by being covered up by dominant genes from the other parent. If we inbreed, however, we provide the opportunity for these recessives to combine in the homozygous state genetically and to emerge as phenotypes. The desirable animals may then be retained and the undesirable ones discarded. If a breeder has an average or below-average herd, their inbreeding will probably result in intensifying poor traits faster than good ones with inevitable deterioration of his stock. The question is sometimes asked as to what degree of inbreeding is permissible. There is, of course, no correct answer to such a question. All one can say is that 25 per cent of inbreeding in herd A might be beneficial while 5 per cent in herd B might be harmful, depending entirely on the genetic complex of the two herds.

If a breeder thinks that he has a particularly good sire and really wants to learn the truth, he can do so by mating this sire to 20 of his own daughters, as suggested by Wriedt. Comparisons between the immediate daughters of this sire and the offspring resulting from breeding this sire to his own daughters will provide the answer to the sire's real worth as a breeding male, for it will reveal his genetic make-up by allowing both his dominant and recessive genes to appear in homozygous form.

Bakewell's Work.—Robert Bakewell, an Englishman, born in 1725, was the first man as far as is known who dared to use inbreeding in a constructive way. He worked with Longhorn cattle, Leicester sheep, and Shire horses. It is said that he secured two heifers and a bull after a great search for just what he wanted, and that his entire herd of cattle was developed from these without any outside blood. His success as a breeder was noteworthy, and is today well known. Culley, writing in 1794, said:

> The great obstacle to the improvement of domestic animals seems to have arisen from a common and prevailing idea amongst breeders that no bull should be used in the same stock more than three years, and no tup more than two; because (say they) if used longer, the breed will be too near akin, and liable to disorders; some have imbibed the prejudice so far as to think it irreligious, and if they were by chance in possession of the best beast on the island would by no means put a male and female together that had the same sire, or were out of the same dam. Mr. Bakewell has not had a cross for upward of 20 years, his best stock has been bred by the nearest affinities, yet they have not decreased in size, neither are they less hardy, or more liable to disorder, but, on the contrary, have kept in a progressive state of improvement.

Since Bakewell's time, his example has been emulated by many breeders. Breeds are best known by means of individuals and families, and most of the latter have arisen as the result of intensifying the characteristics of certain individuals through inbreeding.

Good Results from Inbreeding.—In practically any breed of livestock it is possible to find animals that have resulted from rather intensive inbreeding. As an example, Fig. 160 shows the pedigree of Sybil's Gamboge, a famous Jersey bull.

It will be agreed that this is a rather closely inbred bull. The bull is a double grandson of Imported Oxford Majesty, a triple great-grandson of Royal Majesty, and a septuple great-great-grandson of Gedney Farm Oxford Lad, as well as a triple great-great-grandson of Oxford Ixia 3d, a double great-great-grandson of Lucy 12th, and a double great-great-grandson of Fontaine's Oxford Pride. Royal Majesty founded the Majesty family of Jerseys, which contains many notable show winners and producers. "Get" of Sybil's Gamboge won 14 ribbons at the 1920 National Dairy Show, including one junior champion, three firsts, three seconds, two thirds, two fourths, two fifths, and one sixth, as well as second and fourth in the get of sire.

Sybil's Gamboge has 88 Registry of Merit daughters whose records on a mature basis average 12,234 lb. of milk testing 5.12 per cent. The best record to be found among these daughters is one of 19,239 lb. of milk and 933 lb. of fat made by Sybil's Miss May as a junior six-year-old cow. Sybil's Gamboge also has 21 proved sons.

The late N. H. Gentry, a successful breeder of Berkshire swine, is quoted by Mumford as having said:

> If it is true that inbreeding intensifies weakness of constitution, lack of vigor, or too great fineness of bone, as we all believe, is it not as reasonable and as certain that you can intensify strength of constitution, heavy bones, or vigor, if you have these traits well developed in the blood of the animals you are inbreeding? I think I have continued to improve my herd, being now able to produce a larger percentage of really superior animals than at any time in the past.

The foregoing examples illustrate the fact that not only during the foundation period of the breeds was inbreeding a potent factor for improvement but that it still retains its potency.

Harm from Inbreeding.—In exactly similar manner, one might unearth opinions and examples, both in the past and in the present, that would indicate that inbreeding is an extremely dangerous practice and that anyone using it is liable to encounter serious difficulties. This will not be done, however, for there are many references in the literature of animal husbandry as to the harmful results from the practice of inbreeding.

Experimental Data.—Much experimental work has been done with a view to illuminating the problem of inbreeding. Castle says[1] in regard to some inbreeding experiments with *Drosophila*:

My pupils and I bred brother and sister for fifty-nine generations in succession without obtaining a diminution in either the vigor or the fecundity of the race, which could with certainty be attributed to that cause. A slight diminution was observed in some cases, but this was wholly obviated when parents were chosen from the more vigorous broods in each generation. Nevertheless, the crossing of two inbred strains of Drosophila, both of which were doing well under inbreeding, produced offspring superior in productiveness to either inbred strain. Even in this case, therefore, though inbreeding is tolerated, crossbreeding has advantages.

Bos and Weismann inbred rats for about 30 generations and secured a diminution in both fertility and vigor. King also inbred rats for 25 generations and, according to Hays,[2] found that:

Inbred males in seventh to fifteenth generations were 18 per cent heavier than check males not inbred. Inbred females were about 3.7 per cent heavier than controls at one year old. The variability in both weight at maturity of the fifteenth generation of inbred males and females was about 40 per cent less than among the control animals. King (1918) also studied the effect of inbreeding on fertility, the time of puberty, and the longevity of albino rats inbred by brother and sister mating for twenty-five generations. The average size of litter of all inbred matings was 7.5 rats; and the average litter size for controls 6.7 rats. Inbred rats seemed to reach sexual maturity and to breed slightly earlier than stock females not inbred. . . . The number of sterile animals is not given, but King states that inbreeding did not decrease the productiveness of the animals. Inbred rats lived longer than control animals not inbred. The value of selection in inbreeding animals is concisely illustrated in this painstaking and thorough study of the question of inbreeding.

Reporting on his extensive investigations, Wright says:[3]

There has been an average decline in vigor in all characteristics during the course of 13 years of inbreeding of guinea pigs, brother with sister. The decline is most marked in the frequency and size of litter, in which it is so great that it would have to be accounted for even though the decline in other respects was assumed to be due wholly to a deterioration in the environmental conditions. The decline is greater in the gains after birth than in the birth weight, and greater is the percentage raised of the young born alive than in the percentage born alive.

[1] CASTLE, W. E., "Genetics and Eugenics," p. 221, Harvard University Press, Cambridge, Mass., 1916.

[2] HAYS, F. A., Inbreeding Animals, *Del. Univ. Agr. Exp. Bul.* 123, p. 15, 1919.

[3] WRIGHT, S., The Effects of Inbreeding and Crossbreeding on Guinea Pigs, *U.S. Dept. Agr. Bul.* 1090, 1922, pp. 31–32.

The ability to raise larger litters has fallen off much more than ability to raise small litters.

A comparison of the inbred guinea pigs with a control stock, raised under identical conditions without inbreeding, and derived in the main from the same linebred stock as the inbred families, indicates that the inbreds have suffered a genetic decline in vigor in all characteristics. The decline in fertility is again shown to be marked. Experimental inoculation with tuberculosis has shown that the inbreds were inferior, on the average, to the controls in disease resistance. A study of sex ratio yields results in marked contrast to those obtained in connection with the other characters. There are no significant fluctuations from year to year, no contrast between inbreds and controls, and no indications of change due to inbreeding.

In addition to the points brought out in this bulletin, which indicates genetic decline during inbreeding, extensive experiments have been made in which different inbred families have been crossed together. These are described in another paper (*U.S. Dept. Agr. Bul.* 1121) in which it is shown that crossbred guinea pigs born of unrelated inbred parents are distinctly superior to their inbred relatives in nearly all elements of vigor. A slightly larger percentage are born alive, in small litters at least, and a distinctly larger percentage of those born alive are raised. The young are slightly heavier at birth in a given size of litter and gain much more between birth and weaning. They mature earlier, produce larger litters and produce them more regularly than inbreds. Of the young which they produce, a much larger percentage are born alive, especially in large litters, and even more of these are raised than in the first generation. Their young show a further increase in birth weight and in later gains.

It is believed that the results point the way to an important application of inbreeding in the improvement of livestock. Nearly all of the characteristics dealt with here, like most of those of economic importance with livestock, are of a kind which is determined only to a slight extent by heredity in the individual. About 70 per cent of the individual variation in resistance to tuberculosis and over 90 per cent of that in the rate of gain and size of litter are determined by external conditions. Progress by ordinary selection of individuals would thus be very slow or nil. A single unfortunate selection of a sire, good as an individual, but inferior in heredity, is likely at any time to undo all past progress. On the other hand, by starting a large number of inbred lines, important hereditary differences in these respects are brought clearly to light and fixed. Crosses among these lines ought to give a full recovery of whatever vigor has been lost by inbreeding, and particular crosses may safely be expected to show a combination of desired characters distinctly superior to the original stock. Thus a crossbred stock can be developed which can be maintained at a higher level than the original stock, a level which could not have been reached by selection alone. Further improvement is to be sought in a repetition of the process—the isolation of new inbred strains from the improved crossbred stock, followed ultimately by crossing and selection of the best crosses for the foundation of the new stock.

This method of improvement has not been unknown in the past. In fact, most of the recognized breeds of livestock were developed, more or less uncon-

sciously, in this way. Close inbreeding was practiced by the pioneer breeders—Bakewell, the Collings, Bates, Cruickshank, Hewer, etc. The relatively few promising families and the successful nicks between them were the foundation stock of the breeds. Further development may be expected by the intelligent application of the same principles.[1]

Combining the results described in this and in *Bul.* 1121 there seems no escape from the conclusion that a loss of vigor, especially in fertility, took place as a more or less direct consequence of close inbreeding. The question whether this is an inevitable result of inbreeding or merely a likely one, as well as other phases of the subject, will be discussed after the presentation of further data.[2]

Hughes[3] has recently reported the results of an interesting inbreeding experiment with Berkshire swine. The pedigree of a litter born in 1931 is shown in Fig. 162.

It is evident from the pedigree that full brother-sister matings were made for four generations, *i.e.*, there are only two animals in each of these four generations. Enhancer's Leader 2d and Enhancer's Leader Belle 2d were by the same sire, Enhancer, and out of half sisters by the same sire. There is enough additional inbreeding further back in the pedigree to give these pigs a total inbreeding coefficient (Wright) of 74 per cent.

Hughes gives the following summary of the results thus far achieved:

1. The average number of pigs farrowed, in the inbred litters, has been greater (9.78 pigs per liter) than the average for the Berkshire herd (8.14 pigs per litter for the years 1919–1926).

2. There has been a slight but gradual decrease in the number of pigs farrowed in the inbred litters since 1923. The last litters, however, were the first litters of the sows in question, which tended to be smaller.

3. The types of the pigs in all the inbred litters has been similar.

4. There has been no noticeable color change or structural abnormalities in any of the inbred pigs.

5. The results obtained thus far seem to agree in part with those of Miss King (no noticeable loss in size or vigor) and in part with the results of other workers (there has been a slight decrease in size of the inbred litters).

6. The standard deviation from the mean of the inbred litters is 2.56 with a probable error of ±0.288. The standard deviation from the mean of all Berkshire litters from 1919 to 1926 inclusive is 5.34 with a probable error of ±0.302.

Woodward and Graves (1933) inbred grade Guernsey and grade Holstein cattle—females mated back to their own sire for successive generations, etc. In the Guernseys the birth weights declined, some

[1] *Ibid., Bul.* 1121, p. 49.

[2] *Ibid., Bul.* 1090, pp. 31–32.

[3] HUGHES, E. H., Inbreeding Berkshire Swine, *Jour. Hered.*, **24**(5):200, May, 1933.

deformities appeared, mature weight declined, amount of milk production remained about the same, fat percentage increased. In the Holsteins, birth weights declined, vigor declined, mature weight declined—amount of milk production increased, fat percentage decreased.

Inbred litter (8 pigs) Berkshire, Mar. 24, 1931 Univ. of Calif.	Sir Double Leader 2d 350285	Double Leader of U.F. 350282	Double Leader 4th 331377	Enhancer's Leader 2d 318540, Univ. of Calif.
			Double Leader Belle 331378	
		Double Leader Belle of U.F., 350285	Double Leader 4th 331377	
			Double Leader Belle 331378	
	Miss Double Leader Belle 550285	Double Leader of U.F. 350282	Double Leader 4th 331377	Enhancer's Leader Belle 2d 318539, Univ. of Calif.
			Double Leader Belle 331378	
		Double Leader Belle of U.F., 350285	Double Leader 4th 331377	
			Double Leader Belle 331378	

FIG. 162.—Pedigree of inbred pigs.

Woodward and Graves (1946) make the following statement in their summary and conclusions:

> Generally speaking farmers should not practice inbreeding. . . . An important exception to the general rule should be noted. If a farmer has an outstanding cow or bull, he is justified in inbreeding to the cow or bull in order to obtain a bull or bulls for breeding that will carry a high percentage of the characteristics of the outstanding cow or bull. This course is justified because the fertility of

the inbred bull is not likely to be seriously impaired and any lack of size and vigor in the inbred bull is not likely to be transmitted to the offspring if he is mated to unrelated animals. Continued inbreeding of whole herds, however, is almost certain to be disastrous.

Bartlett, Reece, and Mixner (1939) have inbred Holstein cattle at the New Jersey Agricultural Experiment Station with lethals and deformities appearing in some families, very poor type and red color in other families, good results in some families. They stress the point that rigid selection must be practiced along with inbreeding.

Bartlett *et al.* (1942) reported no harmful effect of inbreeding (up to 20 per cent) on the birth weight, rate of growth, and type of dairy cattle, provided one starts with genetically superior animals and employs rigid selection.

Margolin and Bartlett (1945) from further studies arrive at the following conclusions:

> This paper further confirms earlier work demonstrating that Holstein-Friesian dairy cattle can be inbred without necessarily causing a decrease in body weight or size at any stage, from birth to maturity, as compared to outbred controls of the same blood line, provided the Wright coefficient of inbreeding does not exceed 0.20. Females inbred to a coefficient greater than 0.20 develop normally to approximately first calving age, but show markedly abnormal development thereafter. However, the animals in this group with growth records complete to 72 months of age do not vary significantly in mean weight, height and heart girth from the Ragsdale standard, although they are considerably smaller than the outbred controls.

Tyler *et al.* (1946) found considerable variability in the effects of inbreeding on growth and production of Holstein-Friesian cattle, and their final conclusion is that, "The variation in these partial regression coefficients between sires was large enough that the offspring of some sires might be inbred as much as 25 per cent without any apparent decrease in either body size or milk and butterfat production."

Baker *et al.* (1945) from a study of 88 daughters of the only Holstein-Friesian bull used in the University of California herd for a period of 13 years—24 of his daughters were outbred, F = 0; 8 had an inbreeding coefficient of 12.50 per cent; 27 are of 25.00 per cent; 10 had a coefficient of 31.25 per cent; 13 had 37.50 per cent; and 6 had an average F of 41.66. These investigators' conclusions are as follows: "By means of suitable mathematical and statistical techniques, we have demonstrated a significant, proportionate per cent decrease of size in height, weight and heart girth among the daughters of Bear Valley Ormsby Esther, 518683, with increasing coefficient of inbreeding."

Regan *et al.* (1947) analyzed calf mortality in the 25-year-old California dairy-cattle-breeding experiment and conclude as follows:

> Class I, the control group, contained all animals whose coefficient of inbreeding was 0 to 0.1249; Class II from 0.125 to 0.2449; Class III from 0.245 to 0.3749; and Class IV 0.375 and over. . . . The percentage of abortions in the control group was just as great as in the highest classes of inbreeding. It is concluded, therefore, that the degree of inbreeding has little or no effect on the number of abortions. . . .
>
> Both genetic and environmental factors were found to influence mortality. Total mortality, which includes abortions, stillbirths, and deaths after birth up to 4 months of age, increases with the degree of inbreeding in Jersey females. This is also true for Holstein female calves, but, because of fewer numbers and certain influences of the environment upon mortality, the effect is less marked.
>
> The mortality to 4 months of age for calves born alive increases with an increase in the degree of inbreeding. . . . Individual bulls sire progeny of a characteristic birth weight—light, medium, or heavy—but there is no evidence of a correlation between characteristic birth weight and mortality.
>
> Within the same breed, sex and class of inbreeding, when the progeny of all the sires are combined, there is no significant difference in the mean birth weight between calves that lived and calves that died. Calves with extremes in birth weight, either light or heavy, succumb more readily than calves near the mean weight. . . .
>
> The percentage of mortality varied among the inbred progeny of the different sires. Inbreeding apparently increased the mortality in the progeny of all sires, but the increase over the controls was not significant in the progeny of three of the sires. The mortality among the inbred progeny of all the other sires that had sufficient numbers of offspring was significantly greater than in the controls. It was tentatively concluded that two different lethal genes, conditioning anomalies of the liver and heart, but with no external morphological effects, may have been responsible for deaths in the inbred progeny of two of the sires. These two genes, however, are insufficient to account for all the mortality observed. It seems that more subtle genetic relationships or interactions may be involved in causing most of the mortality.
>
> In inbred calves, the proportion of mortality that cannot be attributed to specific lethal genes, was greatly influenced by management and medication. The mortality was reduced by keeping the calves on fresh, clean ground that had been free from cattle for several months and by the use of sulpha therapy in the treatment of certain infectious diseases.

Dickerson *et al.* (1947) studied the effect of inbreeding on performance in swine and found that for each 10 per cent increase in inbreeding there was an average decline in litter size of 0.2 pigs at birth, 0.4 pigs at 21 days, and 0.5 pigs at 56 and 154 days; in pig weight no decline to 56 days, but 3.6 lb. at 154 days.

Winters *et al.* (1948)[1] report that performance in inbred swine has not deteriorated with inbreeding. "The advance of inbreeding has not been accompanied by any noticeable decline in any of the factors of performance in the lines as maintained." These workers attribute these results to (1) rigorous selection on the basis of performance and (2) a flexible system of mating best to best within lines rather than a rigid pattern of full brother-sister or one-sire herd scheme mating.

Use of Inbreeding.—Inbreeding has been used very little in animal breeding up to the present. Bakewell practiced inbreeding to some extent in England during the eighteenth century, and, when other breeders took up the practice, the foundations for our present breeds were laid. During the past 100 years, however, little animal inbreeding has been practiced. The larger and more influential breeders have used inbreeding to a limited degree, but the belief that there is something inherently harmful in inbreeding plus the justified prohibitions against it in the human have greatly restricted its use, and in consequence many possibilities of more rapid progress in breeding were lost.

In 1905 G. H. Shull at the Station for Experimental Evolution of the Carnegie Institution at Cold Spring Harbor, N.Y., and E. M. East at the Illinois Experiment Station began the experimental inbreeding and hybridization of corn. This work has now developed to the point where the majority of field corn produced is "hybrid" corn. The procedure involves the inbreeding of corn for seven or eight generations, by which time the strain is practically pure or homozygous. Rigid selection is practiced, and the weakest strains discarded. There is always a decrease in yield in these inbred strains. After the best surviving strains have been purified by inbreeding, they are crossed, hybridized, in an experimental way to determine which inbred strains best complement each other. Many systems of hybridizing are in use, including the single cross between two inbred strains, the three-way cross of a third inbred on the result of crossing two other inbred strains, double crosses between two single crosses involving four inbred strains, and top crossing of an inbred strain on a commercial variety. All these systems have certain advantages and disadvantages, the double-cross system being the one most generally practiced.

This hybrid corn has been compared with the mule hybrid in animals. Both of them are excellent in themselves but genetically poor from a breeding standpoint, the mule, of course, seldom being fertile anyway. Only the first generation of hybrid corn should be used for commercial planting, as the second generation generally drops in yield by from 10 to 25 per cent. Properly produced and tested hybrids that are carefully

[1] *Minn. Agr. Ext. Spec. Bul.* 400.

selected for their adaptability for certain regions will yield, on the average, about 8 to 10 per cent more than commercial seed-corn varieties.

The corn breeder is thus analyzing his materials, finding out what they are genetically through inbreeding and record keeping, and trying to fit these known strains together into superior strains. He, of course, has a big advantage over the animal breeder in that self-fertilization can be practiced, making the inbreeding twice as intense as is possible with animals, his number of offspring is many times that possible with even the most prolific animals, and the cost of producing a corn plant is much less than that involved in producing a colt, calf, lamb, or pig.

The man with just average livestock should, of course, not practice inbreeding. The fact that his stock is average means that it has a goodly share of undesirable genes, which inbreeding would make homozygous and therefore worse. For average livestock, outcrossing would seem to be a better system, for unrelated animals would have less likelihood of carrying identical poor genes.

The man with better-than-average livestock should do some inbreeding. The fact that his stock is above the average merit of the breed means that a random-selected, unrelated animal will have a tendency to pull his herd or flock back toward the breed average. Since many breeders still shy at the word *inbreeding,* we will say that the better-than-average breeder should practice *linebreeding,* which of course is a form of inbreeding, but a term which does not have the same fearsome connotations as inbreeding.

Every breeder should try to buy his males in the best available family in his breed. In the present state of our knowledge, the genetically best families in any breed are not easy to know, and one must be wary of advertising and "ballyhoo." Assuming one does buy a sire in a really good family, then, generally speaking, he should try to stay in that family, intensify its good qualities through linebreeding, and weed out the poor genes.

Linebreeding.—Many breeders fear closebreeding (which they often call "inbreeding") but favor linebreeding. This is sound practical judgment. Probably only a tiny per cent of our herds could benefit from closebreeding, a much larger per cent could benefit from linebreeding. What the breeder is constantly trying (albeit unknowingly in many instances) to do is to replace poor genes with good ones—improve his stock. When he gets a great sire (proved so by his offspring) all would be lovely if that sire could be kept alive indefinitely, or at least his testicles through transference to a series of young sires. But eventually he will die and direct samples of his inheritance will be no longer available. Now it is obvious that we can get the closest approach to his good germ cells from his offspring. So the intelligent breeder uses his

sons and grandsons and thereby practices linebreeding. In the last chapter we warned that there was no magic in outbreeding systems, as, for example, crossbreeding. Again let's remind ourselves that there is no magic in inbreeding systems, as, for example, linebreeding. Sometimes breeders set out deliberately to linebreed to certain animals. They draw up a pedigree of an animal to be born 10 years hence by mating certain present animals in line- or closebreeding systems. Often these plans are based on present phenotypes rather than genotypes, and the whole plan is pedigree or paper breeding. These plans seldom work out satisfactorily.

Such general plans can be made to work out very satisfactorily if they are soundly based on present animals' genotypes and enough animals so bred according to plan so that many can be tested and those that meet the test used to continue and build the details of the plan.

Linebreeding should be practiced in only better-than-average herds, seldom if ever, in average or grade herds, but perhaps even here when such breeders turn up with an outstanding sire. In any case, it must be done intelligently and in the light of all the records of performance possible. Some deterioration is to be expected from all inbreeding because even the best of our animals seem to carry some undesirable traits and these as well as their good traits will be intensified (become homozygous). It, therefore, becomes a race between selection and deterioration. Obviously, if a breeder is to win such a race, he must start with good stuff and select intelligently. The annual 500-mi. Memorial Day race at Indianapolis is always won by a good machine (proved good by rigid test, not necessarily by its appearance) piloted by a skillful and daring man who selects his course and his varying speeds intelligently and, to carry our analogy further, who goes to the pits when necessary for an outcross of oil, gas, or new tires.

Linebreeding is not necessarily measured by the inbreeding coefficient as is illustrated in Fig. 163.

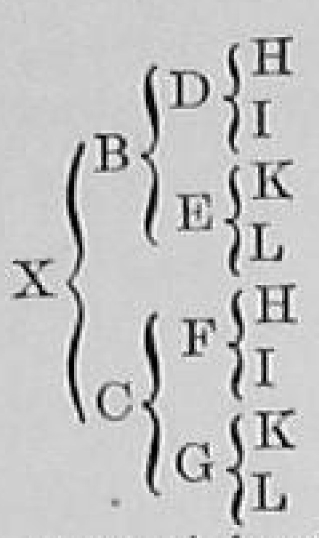
Three of the pedigrees in Fig. 163 show the same amount of inbreeding, but the percentage of "blood" from a certain animal is very different. If we are ever fortunate enough to own a really good sire, we will want to keep his inheritance as intact as possible in our herds.

If we have a good sire, B, his offspring are good presumably, because they get one-half of their inheritance from B, in other words, B's inheritance has been halved just once.

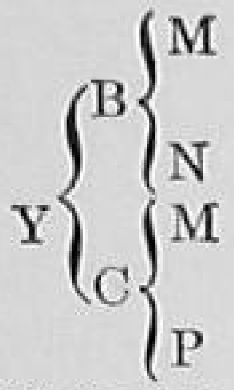
Now, if we get another sire A, unrelated to B, then

A's offspring	A	{ X, Y }
or		
B's granddaughters	B's offspring	{ B, Foundation animals }

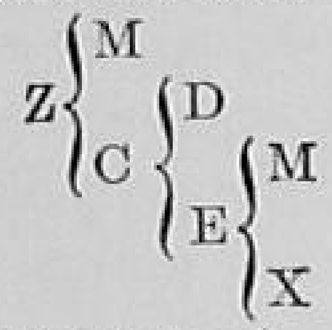
B's inheritance has been halved once more; it is only one-half as strong now, and will continue to be further diluted if we use lines unrelated to B. When we get a good sire, we should try to keep our herd related to him as much as it will stand, and this, of course, involves some degree of



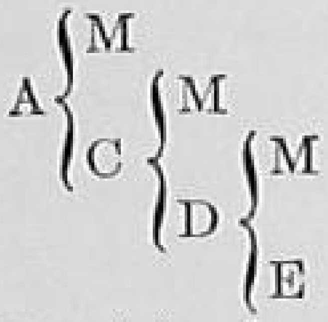
A = 12.5% inbred
25% "blood" from H
25% "blood" from I
25% "blood" from K
25% "blood" from L
Not line-bred



A = 12½% inbred
50% "blood" from M
25% "blood" from N
25% "blood" from P
Line-bred to M



A = 12½% inbred
62.5% "blood" from M
25% "blood" from D
12.5% "blood" from X
More strongly line-bred to M



A = 37.5% inbred
87.5% "blood" from M
Very strongly line-bred to M

FIG. 163.—Pedigrees to illustrate linebreeding.

inbreeding. The following diagram illustrates how a herd or flock might be made to retain its 50 per cent relationship to a good sire B.

B's double granddaughters { Son of B 50% related to B { B, X
12½% inbred
50% related to B { Daughters of B 50% related to B { B, F

It is evident that the above scheme involves some inbreeding, actually some linebreeding. Each animal born is unique as far as genetic make-up is concerned, *i.e.*, there never has been, nor can there ever be, another animal with an identical genetic make-up. When a great sire dies, we can only retain a degree of relationship to him as strong as the relationship evidenced by any of his living descendants. If we have animals that are 50 per cent related to him and mate them, the herd will remain 50 per cent related to the original good sire, but this relationship to him

cannot be increased after he has died. If we have animals that are 75 per cent related to him and mate them, the herd will continue to be 75 per cent related to the good sire. Even five generations of breeding sire to his daughter will only give us an animal 96.875 per cent related to the original sire.

Linebreeding is most generally pointed to some great sire because generally sires through their many offspring become more widely known than do dams through their few offspring. Linebreeding can be pointed to a great female. We think of one well-known and deservedly popular herd which was founded quite largely on one female. She was a great female both phenotypically and genotypically. She had five daughters as good as herself, and this breeder has used two of her sons as herd sires and two of her grandsons. The herd is becoming strongly linebred to this old female and is one of the top herds of its breed.

Closebreeding.—This is the final degree of closeness in breeding starting as we did in the previous chapter with the widest system possible, hybridization, and working up through grading, crossbreeding, outcrossing, and in this chapter linebreeding. Closebreeding is the mating of parent and offspring or full brother and sister. This is the most potent tool available for rendering the genes homozygous. All the cautions stipulated for linebreeding apply to closebreeding and with added emphasis. There, no doubt, are a few animals in every breed which could be closebred, with rigid selection, to advantage. To know unfailingly which these are is difficult. Certainly it can seldom, if ever, be achieved through appearance (phenotype) alone. Closebreeding must be practiced in only the best herds and only on the basis of complete records of performance, our only approach to genotype.

One place where closebreeding would find greater advantageous use is in the production of sires. When a breeder finds himself with a truly great sire, he often looks far afield for his successor, when a better choice is in his own hands. He cannot possibly know as much about some distant herd as he can about his own and he always runs the risk of an unfavorable "nick." Such a breeder might breed his great sire to a few of his own daughters which are members of good cow families and get some males to be tried out as successors to their great sire. This is closebreeding, and these young sires will have 75 per cent of the "blood" of the old sire. Such a bull can be bred to females in the herd which are not descendants of the old sire without any inbreeding at all. If he is used on granddaughters or daughters of the old sire, the offspring will be 15 to 18 per cent inbred, in other words, linebred, and whether good or bad depends on the validity of our original judgment as to the genetic worth of the old sire.

The obverse side of the above picture could be had by breeding the son of a "great" cow back to her to get a sire.

Conclusion on Inbreeding.—From the foregoing, one is forced to conclude that inbreeding in itself is powerless to create either good or bad. If good or bad is present in the germ plasm, inbreeding will sort it out and bring it to light. Closebreeding may be used in the better herds and flocks if accompanied by very rigid selection. However, linebreeding, a less intense form of inbreeding, is decidedly safer. This consists of mating animals of the same general line of descent. Because they are of the same line, they have the same general type of germ plasm and so exhibit the same general set of characteristics. In other words, a linebred herd or flock is extremely uniform, a characteristic almost invaluable (if of a good sort) in animal breeding. In a general way, closebreeding has the greatest permanent genetic possibilities both for good and for harm, whereas outbreeding or mating of animals of no degree of kinship has perhaps the least permanent genetic possibilities for good and the least danger of producing harmful phenotypic results, provided desirable animals form the outcross. It is conceivable, of course, that two animals showing no pedigree relationship for several generations back might have identical genes for one or more characteristics or potentialities, and, that if these two animals were mated, it would, as far as their like genes are concerned, be tantamount to inbreeding. Most people think of inbreeding in terms of the names in a pedigree. Since we can see the names on a pedigree and cannot see the genes in our animals (but only their effects and the picture may be distorted through environmental or genetic influences), this is perhaps the most intelligent way to think about it. But we should keep in the back of our minds the fact that inbreeding is concerned primarily with the genes. If the homozygous state is equal to or superior to the heterozygous state, then we can have as good or better animals through inbreeding and in addition animals which will transmit uniformly.

If a breeder is keen enough in mating his animals and severe enough in culling, he may practice closebreeding. Such pioneering requires both courage and skill. The majority of breeders ought perhaps to seek the middle road, the happy medium. Their desire is to progress, but they cannot afford to take great chances. For such breeders, both their hope and their safety lie in linebreeding, which is an attempt to secure a greater degree of homozygosity of certain desirable genes without running too great a risk of intensifying undesirable ones. This result can be accomplished in a variety of ways.

It is perhaps easier to linebreed to an outstanding male rather than to an outstanding female because of the greater number of offspring of the

former. If one found himself in possession of a really great sire (proved great by his offspring) with many sons and daughters of this sire, he could select two or more of the best sons to mate with the daughters, balancing defects, if present, in the particular matings made. The next generation could be formed by mating the daughters of one sire to a son of another, etc. There is, of course, some danger in the first matings of half brothers and sisters, but, if this stage is passed successfully, there should be no great future danger. The second generation would be double grandsons and granddaughters of the original sire, and the third generation would be quadruple great-great-grandsons and -daughers of the original sire. The fourth generation and later ones would also show some inbreeding to the sons, grandsons, etc., of the two original sons used. These amounts are very small, however. This system should gradually render the genes from the original sire more homozygous, and in general half of the genes of the future herd would be those from the original sire. Pearson and Lush[1] have recently pointed out that essentially this system is being used with marked success by C. C. Good of Ogden, Iowa, in his breeding operations with Belgian horses.

Lush has reported[2] on a herd of beef Shorthorn cattle bred for 20 years without new blood "with the merits of the early good ancestor reasonably well conserved, with the whole herd nearly as like each other genetically as ordinary full sisters, and with the herd still maintaining a reasonably high average of individual merit." A composite pedigree of this herd is shown in Fig. 164.

Another system of linebreeding would result from mating the daughters of a sire to a son of the same sire but out of an unrelated dam, the resulting daughters to be mated to a son of the sire of the daughters again out of an unrelated dam. In this way one is always mating half brothers and sisters and producing double granddaughters of certain bulls. However, outside "blood" is being introduced by selecting the sires from unrelated dams. Various other types and combinations of linebreeding systems are, of course, possible, the aim in all of them being to intensify certain characteristics by rendering them homozygous, at the same time weeding out the homozygous undesirable characteristics. The success or failure of any system of breeding lies first in the genes that the original animals have and second in the breeder's ability to balance defects and mate wisely—in other words, his ability to select. From the genetic viewpoint, some form of inbreeding would be of greatest advantage in cases where

[1] PEARSON, P. B., and LUSH, J. L., A Linebreeding Program for Horse Breeding, *Jour. Hered.*, **24**(5): 185, 1933.

[2] LUSH, J. L., A Herd of Cattle Bred for Twenty Years without New Blood, *Jour. Hered.*, **25**(6): 209–218, June, 1934.

epistasis is involved. In effect epistasis means that the goodness derives from a certain combination of genes. If we outbreed in such a situation, we tend to break up and scatter these desirable combinations of genes. The only way to tend to hold them together in future offspring is through some form of inbreeding.

Our herds were probably formed by selective matings (likes or unlikes) to get desirable combinations of qualities followed by inbreeding to

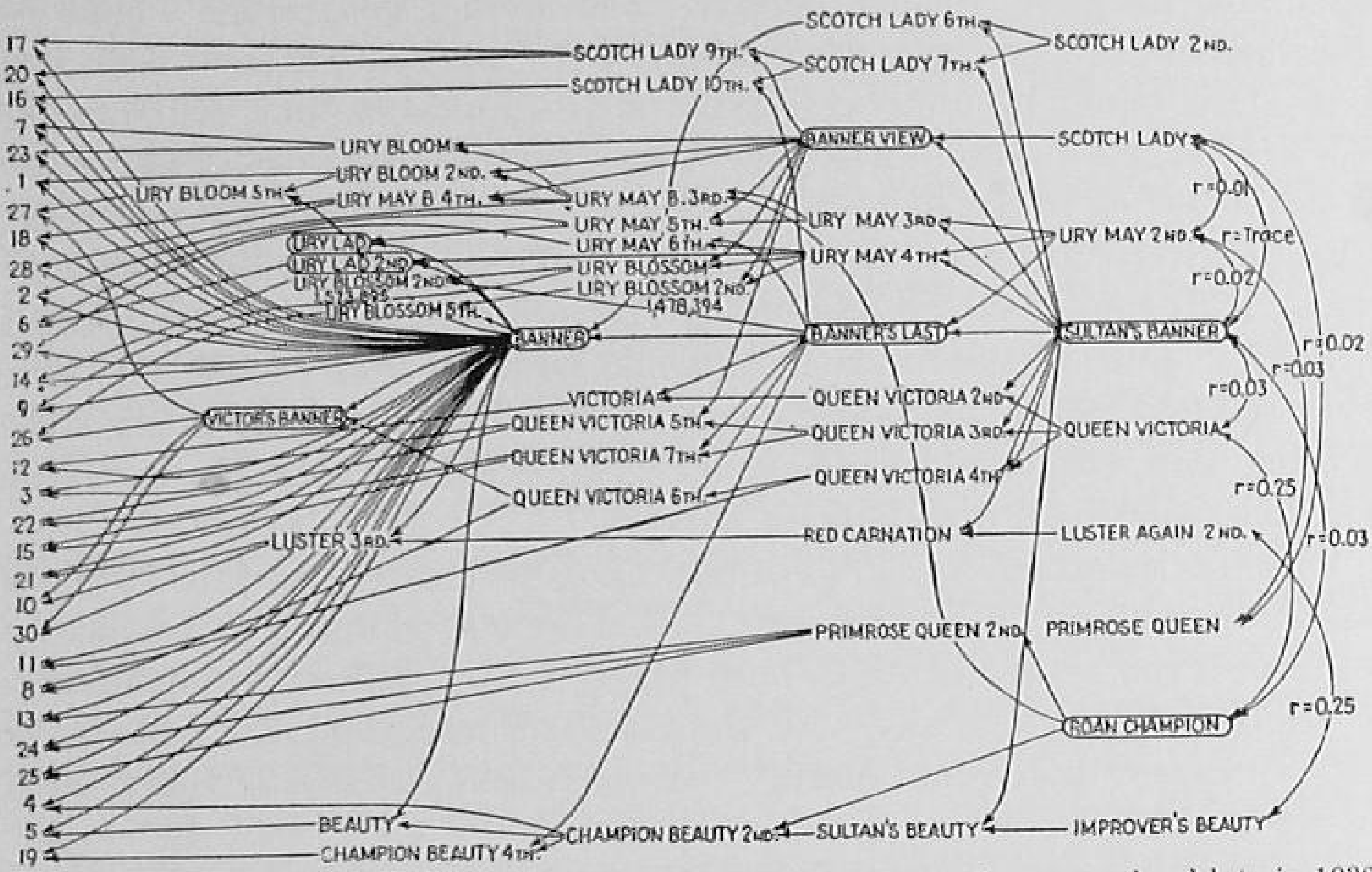


FIG. 164.—Five generations of inbreeding. Pedigree of the entire young herd late in 1932 complete back to the time of Sultan's Banner, and with coefficients of relationship (r) based on the ancestors alive in or near 1900. Each animal is shown but once. If it has more than one son or daughter, an additional arrow indicates that. Selection has not yet had much opportunity to thin out the young herd. When that inevitable culling takes place, many of the lines from Banner will disappear. In the herd 10 or 15 years from now, even though the present plan is continued, Banner may not appear much more important than Bannerview or Banner's Last. In any case he is not apt to be more important than those two combined. (*From Lush, J. L., A Herd of Cattle Bred for Twenty Years without New Blood, Jour. Hered.*, **25** (6):209–218, *June*, 1934.)

render the animals somewhat capable of uniform transmitting ability. The amount of inbreeding being practiced in most breeds at present is very small. Most breeds probably have some good and some poor genetic material. Inbreeding would allow the poor stuff to show itself, and it could then be discarded rather than being carried along in a hidden state, as is likely with outbreeding. No doubt there is some good genetic material in most herds, but it is difficult to know this very definitely without records of performance. Research and discovery of the best within the breeds followed by line- or closebreeding to render the material more homozygous is badly in need of doing. Such purified inbred lines

could then be used for intelligent crossing within the breeds, and they would also be available for crossing between or among the breeds in both fields, thus hastening the creation of better genetic lines. For progress in animal breeding, we need first to know what we now have. When that knowledge is available, it can be used intelligently both to strengthen existing breeds and to create new ones.

Summary.—We have seen in this chapter that animals which evidence relationship by having common ancestors within the first four to six generations of their pedigrees are likely to have received identical genes from their close-up common ancestors. When two such related animals are mated, they may both pass their identical genes to their offspring. Matings involving related animals are called inbreeding, and an inbred animal is likely to be homozygous in more sets of genes than is an outbred animal. Inbreeding creates no new genes but allows those already present to get into homozygous combinations. Inbreeding results in improvement or deterioration, depending entirely on the genes present in the related animals. Only those breeders whose herds are fairly large and of more than average merit should practice closebreeding. Linebreeding should have a greater vogue than it has had in the past.

Inbreeding will be successful (1) if the good genes pretty well outnumber the bad ones to start with, (2) if the breeder has more than average skill in planning his matings, (3) if the breeder can and will practice very rigid selection. Finally, it isn't the system of mating—it's the genes in the animals and the intelligence in the man, and the latter is perhaps also largely a matter of genes.

Inbreeding will uncover undesirable traits in animals, expose them so that they can be discarded. It will create separate more or less homozygous lines which may in themselves lack something of being completely desirable but prove to be very potent for good in crossing between lines or onto heterogeneous material. Good lines may be sorted out from inbred stocks; but when an outcross is resorted to, the good results of many generations of inbreeding will be scattered and lost, *i.e.*, inbreeding must again follow the outcross. Inbreeding will succeed if the genetic complex was good to start with and the breeder's selection is keen enough and ruthless enough to offset probable deterioration.

In closing this chapter, it seems safe to say that animal breeding has lost more through fear of inbreeding than it has lost in any other way. Only occasionally do we get a particularly desirable combination of genes in an animal. Due to the halving and sampling nature of inheritance, outbreeding soon tends to dissipate this original good combination. Each animal is unique, there never has been nor can be another just like it (except identical series). The easiest way to get other animals as near

genetically like the original good one is through some form of inbreeding. Now that the principles involved in breeding systems are becoming better known and understood, it seems reasonable to hope that greater use will be made of inbreeding systems.

Rapid progress in animal breeding will have to wait upon the intelligent use of inbreeding.

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CHAPTER XX

GENERAL CONSIDERATIONS IN SELECTION

Selection is the keystone of the arch in animal breeding. The fact that a breeder's ultimate success depends upon his skill in selecting and mating animals is so obvious that it permits of no argument. It will be recognized immediately also that selection and systems of breeding are bound together so closely that there is no likelihood of being able to separate them. They are but different angles of this same basic problem. We have seen that an animal's ultimate and intrinsic worth depends in the final analysis on the genetic contents of the egg and the sperm that united to produce it. We must, therefore, relate all of our thinking about selection to the ultimate determiners of potentialities—genes and chromosomes—and it hardly seems necessary to add that whether or not an animal with a good hereditary complex actually develops into a desirable individual depends in turn on the type of environment, especially feed, care, and management, which is provided. If our selection is successful, if the animals we breed, in other words, are superior in the qualities that enable them to perform their respective functions successfully and profitably, it will be because their good genes have had an opportunity to express themselves in a suitable environment.

Selection is nothing new. It has been going on for over a billion years, or since the first forms of life appeared on this planet. This is called *natural selection* and is the idea on which Charles Darwin formulated his theory of evolution. For millions of years before man even appeared on the scene, nature was busy putting the genes together into new combinations (variations). Some of these new combinations were successful, giving rise to new types of life that were adapted to the given environment. They, therefore, prospered and multiplied. The unsuccessful combinations were those giving rise to animals that were ill-adapted to their environment. They could not live and prosper and therefore left few or no progeny. Nature was ruthless, her one criterion was fitness, and on the dual bases of variation and fitness she has peopled the earth with myriad forms of life. A long, long succession of successful variations finally produced man himself.

One of man's early and most far-reaching accomplishments was the domestication of plants and animals. When this had been accomplished,

nature's passive selection was supplanted by man's active artificial selection. The latter has been going on for some 5,000 to 10,000 years; and, in spite of certain cynical opinions to the contrary, it has had a truly remarkable degree of success. For proof of this statement, all we need do is contrast a wild boar and a champion barrow; a Texas Longhorn and a grand champion steer, a mouflon and a modern sheep, Przhevalski's horse and a modern Percheron; an early type cow and a modern dairy queen. Both in looks and utility such a wide gulf separates these extremes that one marvels it could be bridged in such a short space of time. Some critics aver that there has been no progress in livestock breeding during the past 200 years, that all our gains in animal form and function are due to better feeding and management. That the latter have played a large part no intelligent person would wish to deny, but to give them the whole credit seems unjustified. It is tantamount to saying that all livestock breeders' efforts at selection have been fruitless, that as a group they have not increased to any degree the relative frequency of good genes or been able to discard any bad ones.

If one wishes to maintain that selection methods have not been 100 per cent efficient, he would have ample justification for his position, but to deny any progress in breeding for the past two centuries is simply not in keeping with facts, and before being too critical of breeders of the past, one should, in fairness, recognize the handicaps under which they worked. The mechanism of reproduction was the last field tackled by the physiologist, and its complete functioning in terms of the immediate organs concerned and the remote controls situated in the endocrines is only now beginning to be understood in a relatively complete manner. Likewise the mechanism of hereditary transmission has been understood for only 50 years, and its real use as a tool in creating better plants and animals was begun only 30 or 40 years ago. Mass or phenotypic selection has brought us a long way from the crude and inefficient types of animals with which man began. It can be admitted that "ox-cart" or "horse-and-buggy" methods of selection need modernizing without belittling the accomplishments and tools of those who have passed on.

For a long time, selection in all classes of livestock was based upon individual appearance, that is to say, ideals of bodily form were set up after which the breeder tried to mold his own herd or flock. Many influences helped to shape these ideals, one of the most important of which was the show-ring standard. It was thought, in other words, that there was a relation between form and function with horses and dairy cattle as well as with meat animals. Selection was based largely on anatomy. Gradually, however, it became apparent that, in dairy cattle especially, there was no necessary correlation between type and produc-

tion, between external anatomy and internal physiology. Selection then shifted its base somewhat by including a consideration of performance at the drawbar, at the milk pail, or in the feed lot. Selection, in other words, came to include physiological functioning as well as anatomy. Finally, however, it became apparent that an animal's own performance was also far from a perfect guide to its transmitting ability.

In recent years, therefore, we have heard much of progeny-performance tests as the only safe measure of an animal's breeding merit. We still pay attention to type, anatomy, or external appearance; we still pay attention to performance, physiology, or internal activity; but to these criteria of selection we have now added a consideration of how the animal actually performs in transmitting its own desirable qualities. We still pay as much attention as possible to individual appearance and individual performance. We want both these things in our breeding animals, but we have slowly come to realize that having either one or both does not guarantee that an animal will be a good transmitter. If we can make our animals' pedigrees complete enough in terms of records of accomplishments (both as individuals and as transmitters) of the direct ancestors in the pedigree and a goodly share of the collateral relatives, we can predict with a fair degree of assurance how the animals will transmit. However, the final and only sure test of an animal's breeding worth is now recognized to reside in the quality of its offspring. Good type, good performance, good pedigree (in terms of records) are indications of breeding merit, but the only assurance of breeding merit resides in the offspring themselves.

Variation, the Base for Selection.—The breeder's stock in trade is variation. The milk production, butterfat test, and total butterfat of cows; the rate of gain and quality of carcass in fat stock; the amount of wool, the ability and willingness to pull, the color pattern, the fertility rate, the type, the length of useful life (we could go on almost indefinitely) do show considerable variation. Selection is the breeder's attempt to seize and perpetuate such favorable variations as come his way. If a Holstein is black and white, we know it has at least one gene *B*—what the other gene of this pair is, we cannot tell by inspection; *i.e.*, one black Holstein may be *BB*, another *Bb*. Likewise, two Holsteins may each produce 10,000 lb. of 3.6 per cent milk, but this is no sure ground for assuming that they have identical sets of genes. One of these Holsteins may transmit very well to her daughters—the other one very poorly.

We do not know how many genes each species of our farm animals has. A recent estimate of the number in man by Spuhler (1948)[1] based on total length of human chromosomes compared to Drosophila and on esti-

[1] SPUHLER, J. N. "On the Number of Genes in Man," *Science*, **108**:279–280, 1948.

mated mutation rates in the sex chromosomes yields the limits of 20,000 to 42,000 genes in the human. Possibly the number of genes in our farm animals is something fairly comparable. It is unlikely that we can ever know very accurately what genes any animal has. Selection, therefore (marshaling favorable genes) must be done indirectly.

Since all living forms are probably the result of an evolutionary process, they may all still have some genes in common and the more closely related individuals are, the more genes will they have in common. An amoeba and a man may have some genes in common, though probably not many. A monkey and a man no doubt have more genes in common (sometimes, apparently many). A Chinese and an American no doubt have still more genes in common, two Americans still more, two Smiths still more, the two "coughdrop" Smiths still more, and identical twins have all their genes in common, except for the slight possibility of mutations.

Breed differences are gene differences. Breed A and breed B, no doubt, have many (or most) genes in common. But they have enough different genes so that they are set off into two distinct breeds. If 1 in 200 Angus calves is born red, then the frequency of the *b* gene must be about 0.07 (*bb* or b^2 being 0.07×0.07 or approximately 0.005 per cent) and the frequency of the *B* gene is, therefore, 0.93. Then pure (homozygous) blacks, *BB*, are 86½ per cent; *Bb* are 13 per cent and *bb* are ½ per cent, since the zygotic ratio is the square of the genetic ratio. Shorthorns, however, and Herefords, while no doubt having many of the same genes as do Angus, are 100 per cent *bb*, having no blacks. By selection the frequency of the *B* and *b* genes in the Angus breed could be changed in either direction. If the selection was for more red (more *b* genes), then it would move up to 1 per cent red calves when the breed would be 81 per cent *BB*, 18 per cent *Bb*, and 1 per cent *bb*; then up to 10 per cent red calves when the breed would be 48 per cent *BB*, 42 per cent *Bb* and 10 per cent *bb*; then up to 25 per cent red calves when the breed would be 25 per cent *BB*, 50 per cent *Bb* and 25 per cent *bb*; etc. If there is no selection for one gene or against another, the original frequencies of the genes will remain just as they are.

While breeds have many genes in common, they also have many which are different. Breeds may be homozygous dominants (for some genes), homozygous recessives, or be of any degree of heterozygosity. The members of a breed in one section of the country (descended largely from a certain foundation) may be genetically quite different from the members of that breed in some other section of the country. The genes in two herds in the same section of the country may be quite different in the relative frequency of certain genes. The early success of selection in

molding animal and plant types toward an ideal led to a belief that selection had practically no upper limit. The discovery of the hereditary mechanism as resident in the genes finally dispelled this illusion. This was brought about largely through the work of Johannsen with the self-fertilizing garden bean. From a mixed population, he selected plants that bore large seed and others that bore small seed. Attempts at selection within these "pure lines," however, proved unavailing. Selecting large seed from the large line gave no larger seed, on the average, than did small seed from this line. Likewise, the selection of small seed from the small line gave no smaller seed, on the average, than did large seed from the small line. Johannsen designated these as "pure lines," *i.e.*, pure from a genetic standpoint. Small seed from the large line was small because of environmental effects, but genetically these small seeds were just like the large seeds in the same line.

Selection, therefore, did prove to have an upper limit, and selection within a "pure line" was not effective. Thus, for the first time, it was fully realized that the effectiveness of selection was entirely dependent on the nature of the hereditary units. If a quantitative character depends on two sets of genes *A* and *B* and we start with a heterozygous generation *Aa Bb*, we can get out a line that is *AA BB* or *aa bb*, thus showing the character to a greater or less degree than did ancestors. When we get a line that is *AA BB*, thus showing the character to a greater degree, we cannot go beyond this point. This is a pure line which, under optimum environmental conditions, will always breed true.

This general principle is applicable to all living forms. In our livestock, it is probable that most commercially desirable characters are of a quantitative sort and probably controlled by scores or hundred of genes. What we are attempting to do in selecting is to develop our animals into "pure lines" or as close to this as we can get with unisexual animals. The task is not an easy one because of the time necessary and the complications involved in dealing with large numbers of genes, but knowing the underlying scientific basis will at least enable us to chart our course more intelligently. Dealing with large numbers of genes simply means that it will take a long time to get them sorted out into the desired homozygous forms, but we can have the comfort of knowing that when we once get them sorted out they will remain in that condition indefinitely except for an occasional mutation. There seems to be a growing belief, however, that the best animals phenotypically may not be the most homozygous—in other words, that an *Aa* animal may be better phenotypically than either an *AA* or an *aa* animal. If this idea proves to be true, it will, of course, have a very marked bearing on systems of breeding.

This brings to mind the importance and gravity of the decision to

introduce a certain male into our breeding plans. When once we bring a male into our herd or flock, his influence, good or bad, is apt to remain with us for some time. When once his genes are put into our "hereditary mix," they remain there more or less indefinitely. Probably most males will bring in some undesirable genes, and, if there are not too many of them, we can hope to rid ourselves of them in a reasonable length of time. If a male brings a host of bad genes, they may plague us through many generations.

As we saw earlier, the genes may act in a variety of ways. They may show additive or cumulative effects. If in sheep, for example, genes *A*, *B*, *C*, and *D* stood for 1 lb. of wool each and *a*, *b*, *c*, and *d* for ½ lb. each and a breeder has a flock that was *Aa Bb Cc Dd*, he could by interbreeding select out lines that were *AA BB CC DD* (shearing 8 lb.) or *aa bb cc dd* (shearing 4 lb.). Our assumption is that these genes act additively so that when *AA* replace *aa* wool production goes up 1 lb. It seems certain that much inheritance for commercially valuable traits in our livestock is of the additive type, though far from all of it.

Dominance effects may be misleading. In the above example if *A* (1 lb. of wool) were dominant over *a* (½ lb.) then substituting a large *A* for one of the small *a*'s in *aa* animals increases yield by ½ lb., but not when substituted for the small *a* in *Aa* animals. *AA* and *Aa* animals yield alike but do not breed alike—we will make some mistakes in selecting because we can not readily distinguish between the *AA* and *Aa* individuals. Epistatic effects, dominance between pairs of nonallelic genes, behave in a similar fashion and are a hindrance to selection because to have the desired effects we must keep certain combinations of genes together, a hard thing to do because of the principle of independent assortment.

Genetic variation is then of three sorts—additive, dominance, and epistatic. The first sort presumably shows its presence whenever it occurs in a phenotype. The offspring will, therefore, average halfway between the phenotypes of their parents. Dominance and epistatic variance, while genetic and hereditary in the broad sense, does not behave in this simple additive way, and the phenotype does not tell so complete and simple a story of probable genotype as it does when the inheritance is of the simple additive sort. If a good quality is due to simple additive inheritance, it can be seized and enriched by selecting and mating parents which show the quality in increasing amounts. If the quality is influenced by dominant or epistatic genes, it will not necessarily be passed to all offspring because of the halving and sampling nature of inheritance. Finally, an animal with an average or mediocre genotype may, through the stimulus of excellent environment, perform fairly or very well. But

these environmental, dominance, or epistatic effects are not necessarily passed on to offspring which may fall far short of their parents' accomplishments.

Technically, variation is called variance, which is the average of the squared deviations of all the variates. The square root of the variance is the standard deviation represented by small Greek sigma or σ. Total observed variance or σ_O^2 is, therefore, made up of four portions: additive, σ_G^2; dominance, σ_D^2; and epistatic, σ_I^2; and environmental variance which is represented by σ_E^2.

Breeders try to select offspring from their better animals on the basis of how these animals look and/or behave, their phenotype. If the variance were entirely caused by additive genetic differences (none by environment, dominance, or epistatic effects) the phenotype of the parents would be their genotype, the offspring would average the same as the average of their selected parents and the entire selection differential would be achieved. The selection differential is the difference between the average in any quality of those selected to be parents and the average of the whole population in which they were born. If the average litter size in a herd of hogs this year was 8 pigs and we saved pigs from litters of 10 pigs, the selection differential would be 2 pigs. If this were all due to additively genetic variance, next year's litters, while variable, would average 10 pigs per litter. Animal breeding would then be too easy to offer much of a challenge.

Actually much of the variance in the commercially valuable traits of our animals is from environmental, dominance, and epistatic causes. All observed variance is σ_O^2, and this is made up of genetic σ_G^2, dominance σ_D^2, epistatic σ_I^2, and environmental σ_E^2 fractions. What portion of the phenotypic superiority of parents we are likely to get in their offspring consists of the genetic variation σ_G^2 divided by the sum of all the sorts of variance, plus a small amount of the epistatic variance in the first generation.

Methods of estimating heritability all depend in one way or another on the amount of resemblance between relatives as compared to resemblances between animals selected at random from a population. Another way of saying this is that heritability can be determined by comparing the amount of variation among animals selected at random with that found among animals of known relationship. Where possible, the best method of ascertaining heritability is to compare the variation in a random-breeding population where both hereditary and environmental variation exists with that in pure lines where practically all the variation is environmental in origin. Unfortunately, this is not feasible in farm animals except in the case of cattle where identical twins and ordinary

twins can sometimes be so used. Estimates of heritability based on the resemblances between relatives are fraught with the danger that relatives may resemble each other both because they have similar genes and because they have been exposed to similar environmental influences. Lush discusses[1] the use of parent offspring resemblances as follows:

The resemblance between parent and offspring is the most widely useful method, but is likely to include some environmental correlation between parent and offspring. Also it will include something from the resemblance of the offspring to the other parent, if mating were not random. In using this method the procedure is as follows: (1) observe the correlation between parent and offspring, (2) subtract from that the environmental contribution, (3) double the remainder, and (4) divide by one plus the correlation between males.[2] The second step is always likely to be difficult, and the fourth will be unless the deviations from random mating are known more exactly than is usually the case.

A useful dodge which makes steps two and four unnecessary is to divide the mates of each sire into a high and a low half on their own performance, combine the data for all sires, divide the difference between the daughters of the high and the low halves by the difference between the two groups of dams and double the result. This measures the additive portion and a bit of the epistatic portion of the differences between such dams as were mated to the same sire. It leaves unanalyzed the average differences between the groups of cows which get mated to different sires. A similar division of the offspring of the high and low sires mated to the same dam would answer as well in principle but, because of the usually small number of offspring per dam, is rarely possible with farm animals.

Half-sib correlations are also used in determining heritability. Wright, using a strongly inbred line and a control, outbred line of guinea pigs, measured the average likeness between parents, between parents and offspring, and between litter mates and was able to separate the variance in amount of white spotting into three categories: (1) that due to heredity, (2) that due to environment common to litter mates, and (3) that due to environment not common to litter mates. The results showed that, while the variance due to environment was nearly the same in the two groups in actual units, it made up 97.2 per cent of all the variance in the inbred group and only 57.8 per cent in the control, or outbred, group. In other words, the hereditary variance in the inbred stock was only 2.8 per cent, while in the outbred stock it amounted to 42.2 per cent.

[1] Lush, J. L., "Animal Breeding Plans," pp. 93–94, Collegiate Press, Inc., of Iowa State College, Ames, Iowa, 1945.

[2] This should be the genetic correlation (coefficient of relationship) if the departures from random mating were of the inbreeding kind, but should be the actually observed correlation if the mating choices were based on each animal's own individuality for the characteristic being studied. One will rarely be certain about this.

Many studies on the heritability of various characters in farm animals have been made during the past two decades. Most characters which are important in the production of profitable livestock have been found to have heritabilities in the range from 15 to 50 per cent, with a few estimates above and below this range. Summaries of actual heritability estimates will be given in later chapters in connection with the discussion on selection in the various types of livestock.

As will be seen later, rather different estimates of the heritability of the same character have sometimes been obtained in different studies. Possible reasons for this diversity quickly become apparent when we remember that heritability depends upon the relative amount of variation which can be ascribed to heredity and environment, respectively. Variation in the actual amount of variance due to either of these causes will greatly affect heritability estimates.

The amount of genetic diversity in the populations sampled will have a great influence on heritability estimates. Increasing genetic purity leading to less genetic variation results in lower heritability estimates. The work of Wright previously referred to in which heritability of degree of hair-color spotting in guinea pigs was greatly decreased in inbred strains is an example of this. The more recent work of Hetzer *et al.* (1944) in which apparent heritability of type in swine was found to be about 90 per cent when three widely different types were considered as one population, but only 38 per cent within strains is a further illustration of the same general principle.

Conversely, a decrease in variation of environmental origin will lead to higher heritability estimates. This points out the necessity for maintaining fairly uniform environmental conditions if breeding operations are to achieve maximum success.

Finally, small numbers of animals have been included in some studies, and some of the disagreement in the estimates is doubtless due to sampling errors.

A heritability estimate is really nothing more nor less than an estimate of the average correlation between genotype and phenotype. A high heritability indicated a high correlation, which in turn means that an animal is probably similar genotypically and phenotypically. In such cases progeny tests and family selection are unnecessary. In the majority of cases, however, heritability is relatively low, and information from progeny tests and the performance of relatives will be helpful in estimating the probable genotype of an animal. Picking the better representatives in a herd or flock to be the parents of the next generations is not enough to ensure progress. Because so much of the variance is other than simply additively genetic in nature, we must broaden the base of selection to

include as many of the close relatives as possible and select from good phenotypes which, according to the nature of the performance and transmitting abilities of their near relatives, are probably also good genotypes. If the maternal great-granddam was a productive female and had several good offspring among them, the granddam, which was by a good proved sire, and this maternal granddam was in turn a good producing female and got good offspring among them, the dam, which was by a good proved sire and the dam herself was a good producing female and has gotten some good offspring, then her present offspring which we are considering, if by a good proved sire, has a reasonable expectation of being a good one. In short, selection is likely to be more successful if the six animals making up the bottom line of the pedigree for three generations back are not only good phenotypes, but whose genotypes have also been tested through their offspring and found to be good.

Characteristics of a Livestock Population.—The numerical data as to numbers and values of animals in the various classes of livestock are given in Tables 1 and 2. Dividing the total value in 1949 by the total number gives us an average value of $95 per head for all classes of animals combined. The specific values for each class are listed in Table 1. The modest value of the average horse, mule, cow, sheep, or pig should provoke serious thought on the part of livestock breeders. These average values indicate that billions of dollars worth of product are being produced annually in the United States with low-grade, inefficient animals. Such economic waste should be checked as soon as possible.

The average dairy cow is said to produce 5,000 lb. of milk and 200 lb. of butterfat yearly. In 1947, 775,000 cows in Dairy Herd Improvement Associations (D.H.I.A.) averaged approximately 8,700 lb. of milk and 350 lb. of butterfat. According to the Bureau of Dairy Industry, the feed cost per pound of butterfat in the latter group of cows was 43 cents, while in cows producing only 200 lb. of butterfat, the cost per pound was 60 cents. Speaking generally, dairymen who test their cows are a selected and superior group of men. They pay more attention to breeding, they grow their young stuff better, they farm and they feed at higher levels than the average. So part of the increased production of D.H.I.A. cows is, no doubt, due to better environmental conditions, part is due to better inheritance, and how much, on the average, environment plays and how much inheritance, no one can say. D.H.I.A. figures show conclusively that "income over feed costs" mounts steadily with increasing production. True, the high-producing cow eats more feed than the low producer, but a smaller percentage of her feed needs to be used for maintenance. Or to put it another way, the higher producing cow

produces more product per pound of feed consumed and for this reason is more efficient and more profitable.

It should be remembered that an average is a mid-point. If the average production of all cows in the United States is 5,000 lb., of milk, then about half our cows must produce less than 5,000 lb. of milk per year. To people living in a good dairy area, this is almost unbelievable.

Table 34 shows the distribution of 216,489 cows on which dam-daughter comparisons were secured in proving the first 25,000 bulls in D.H.I.A. testing.

The average butterfat production of all the dams in Table 34 is 376 lb.

TABLE 34.—DISTRIBUTION OF COWS' RECORDS USED IN PROVING THE FIRST 25,000 DAIRY SIRES BY THE BUREAU OF DAIRY INDUSTRY*

Dam and daughter pairs	Number of sires used	Dams' butterfat, lb.	Daughters' butterfat, lb.	Bull's Equal-parent Index†
94	16	188	243	298
324	52	215	254	293
1,351	182	240	271	302
4,483	579	264	292	320
10,365	1,286	289	310	331
19,317	2,301	313	329	345
30,462	3,507	338	346	354
40,308	4,479	362	365	368
39,536	4,464	387	383	379
30,924	3,466	411	403	395
20,304	2,363	436	421	406
10,888	1.299	460	438	416
5,321	626	485	451	417
1,799	238	510	472	434
544	75	535	474	413
283	40	560	496	432
106	13	584	535	486
56	7	610	436	462
24	4	637	476	315
216,489	25,000	376 Av.	375 Av.	

* Adapted from data in D.H.I.A. Letter, Vol. 24, No. 12, December, 1948.

† Indexes will be discussed at length later. The formula for the Equal-parent Index is twice the daughters' average minus the dams' average. This places daughters just halfway between the parental levels.

It will be seen that the greatest number of cows (79,844) is in this group and that the number in the other groups tapers off fairly regularly as we approach the upper limit and not so regularly as we approach the lower limit because the poorer cows are disposed of early. In short, most

animals are average animals—there being fewer very poor or very good ones. The breeder's job is to find the upper half of his herd in transmitting ability and to save his replacements from these better-than-average females which are in better-than-average cow families and see to it that they are by better-than-average males. Only in this way can improvement be brought about.

It will be seen in Table 34 that the dams are arranged from low to high by 25-lb. intervals. They start at 188 lb. and proceed upward in a straight line to 637 lb. Their daughters start at a higher level and end at a lower level. When their daughters' production is fitted to a straight line by the method of least squares, the daughters' production is found to

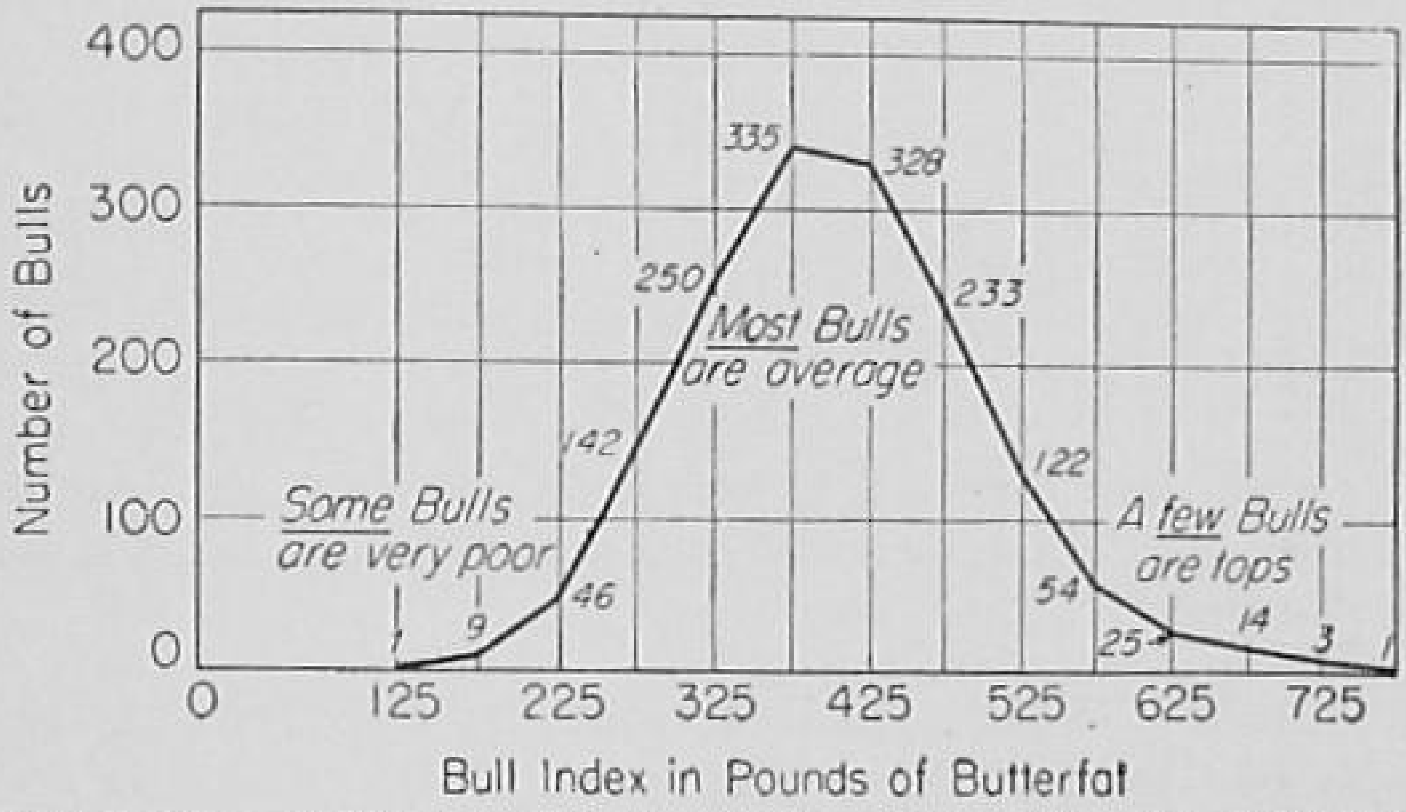

FIG. 165.—Distribution of Holstein-Friesian bulls. (From Vol. 15, *Holstein-Friesian Red Book.*)

start at 247 lb. and to end at 541 lb. The regression of daughters on dams in an unselected population is known to be 0.5. This means that these daughters should start at 275 lb. and end at 512 lb. They actually start at a lower figure and end at a higher one. This would seem to indicate that there is effective selection now used in some D.H.I.A. herds. The poorer herds seem to use below-average sires and the better herds to use above-average sires. If the environment were the same for all herds, we would know this to be the case. Some of this possible hereditary difference may actually be due to environment, the poorer herds holding down production of both dams and daughters through poor feeding and management and the better herds boosting production by superior feeding and management. For the data in Table 34, the sires' transmitting levels (Equal-parent Index) start at 305 lb. and end at 449 lb., instead of running straight across on the 375-lb. level as they would do if all environmental conditions were similar and there were no effective selection. The above data shows that, so far as milk production is concerned, most cows are about average and that they grow

smaller in numbers as the extreme of low production or high production are approached.

A few years ago we studied the transmitting abilities of some 1,563 Holstein bulls. From their daughter-dam comparisons, the apparent transmitting qualities of these bulls were known. Their distribution is shown in Fig. 165.

In Table 35, we show the distribution as regards type classification in our dairy breeds.

TABLE 35.—DISTRIBUTION OF TYPE IN DAIRY CATTLE

Classification	Ayrshire	Brown Swiss	Guernsey	Jersey	Holstein	All	%
Excellent	729	130	290	2,746	1,401	5,296	2.2
Very good	5,676	2,264	3,716	29,995	15,687	57,338	23.4
Good plus	8,259	4,683	8,494	49,664	35,261	106,361	43.4
Good	3,923	2,429	4,672	20,623	30,995	62,642	25.6
Fair	611*	248	818	2,908	8,306	12,891	5.2
Poor	......	3	115	60	382	560	0.2
	19,198	9,957	18,105	105,996	92,032	245,088	100.0

* Includes any classified "Poor."

Again we see in Table 35 that the animals distribute themselves in a fairly regular way around the average.

The main purpose of calling attention to the distribution of any population around its mean is to portray the principal problem involved in improving our livestock. As we have already said, our task is to find the better females and get them bred to the better sires. Up to the present, it has been a case of average females being bred to average sires with the foreordained result of getting average offspring.

Results similar to the above for dairy cattle would no doubt also be found for our various classes of fat stock were records available. That animals vary is an observation that none can miss. When the quality being considered is one determined by the interaction of many sets of hereditary determiners or when it is one that is easily influenced by environmental factors or both, the population distributes itself around the mean in a fashion closely resembling a normal curve, as is illustrated in Fig. 165.

From the very beginning, animals of any class have probably tended to vary about their respective mean or average in any quality. The fact that our animals have been improved down through the ages signifies that man has been able to select from the upper half of the population. In this way the average has been moved upward by almost imperceptible

stages. Now that some of the facts regarding the principles of heredity are known, a somewhat more rapid shifting of the average toward higher goals should be possible. It must be remembered, however, that gradual progress made through the centuries may have limited somewhat the working range of animal breeders. For example, further improvement in the egg-laying ability of a 250-egg strain of chickens may be more difficult than in a wild strain laying one clutch a year. In general, the means effecting further improvement would seem to consist of two things: (1) getting more accurate and complete facts about the various qualities of our animals and using the facts more intelligently by arriving at an animal's probable genetic value from a consideration of its close relatives as well as the animal's own qualities; *i.e.*, broadening the base of selection; and (2) being more careful to separate, in so far as possible, genetic from environmental variations. We will probably continue to find that our animals will vary around their mean. How to locate the favorable genetic variations will continue to be our main problem in selection.

Changing Gene Frequencies.[1]—Since genes determine characters, breeders, in selecting for certain things, are actually trying to influence the proportion of different genes in their stock. Wright, in studying the coat colors of the parents of 3,000 Shorthorn cattle, found that 47.6 per cent were red, 43.8 per cent were roan, and 8.6 per cent were white. Since this is a character seemingly controlled by one pair of genes lacking dominance, we know that to the 8.6 per cent of white genes showing as white and to the 47.6 per cent of red genes showing as red must be added one-half the roan value 43.8/2 or 21.9 (roan being *Rr*), in order to get the frequency of the white and the red genes in the population. Thus, 47.6 + 21.9 = 69.5% red genes and 8.6 + 21.9 = 30.5% white genes in the population. Now, if the population had been mating at random, we would have had

	69.5 *R*	30.5 *r*
69.5 *R*	48.3 *RR*	21.2 *Rr*
30.5 *r*	21.2 *Rr*	9.3 *rr*

or

48.3 *RR*:42.4 *Rr*:9.3 *rr*

instead of

47.6 *RR*:43.8 *Rr*:8.6 *rr*

This slight discrepancy shows that mating was not at random but that there was a preference on the part of breeders for roan.

[1] See *ibid.*, pp. 64–71.

Generally, q is used to represent the frequency of one gene and $1 - q$ its allele, and since in random mating the proportion of different zygotes will be the square of the gametic ratio, the ratio of zygotes becomes:

$$q^2 : 2q(1 - q) : (1 - q)^2$$

If either the first or the last term is known, the others can be computed. If 1 per cent of Holstein calves were born red in color, then red, *rr*, or $(1 - q)^2 = 0.01$ and $(1 - q) = 0.1$ and $q = 0.9$. So under this assumption 81 per cent of Holsteins would be pure for black, homozygous *BB*; 18 per cent heterozygous, *Bb*; and 1 per cent would be red. In other words, if 1 per cent of Holstein calves are born red, then 1:5 or 6 black Holsteins are heterozygous for color.

	q^2 *AA* 0.25	$2q(1 - q)$ *Aa* 0.50	$(1 - q)^2$ *aa* 0.25
q^2 *BB* 0.25	0.0625 *AA BB*	0.1250 *Aa BB*	0.0625 *aa BB*
$2q(1 - q)$ *Bb* 0.50	0.1250 *AA Bb*	0.2500 *Aa Bb*	0.1250 *aa Bb*
$(1 - q)^2$ *bb* 0.25	0.0625 *AA bb*	0.1250 *Aa bb*	0.0625 *aa bb*

FIG. 166.—Independently segregating genes *A* and *B*—frequency 0.5.

This principle applies also to independently segregating, nonallelic gene pairs. This can be shown by the usual 9:3:3:1 dihybrid ratio. If genes *A* and *a* have a frequency of 0.5, genes *B* and *b* also a frequency of 0.5, then they will recombine as shown in Fig. 166.

This formula could be extended to n genes by serial multiplication of the squared binomial of each independently segregating gene,

$$[q_A A + (1 - q_A)a]^2[q_B B + (1 - q_B)b]^2, \text{ etc., to } n$$

Thus we can see that with two pairs of genes of equal frequency (0.5) we would have 1:16 chances of getting an animal pure for both pairs of dominant genes (*AA BB*). This is calculated according to the formula q^{2n} (n being the number of pairs of genes involved). Thus in Fig. 166, q was 0.5 and n pairs of genes was 2, so $0.5^4 = 6.25\%$, or 1:16 chances. With q at 0.4 and five pairs of genes, we would have $0.4^{10} = 0.0001$, or

1:10,000 chances of getting an animal homozygous for all five pairs of genes whose frequencies were 0.4. If the gene frequencies had been 0.6, our chance would have been 1:166; if it had been 0.8, our chance would have been 1:about 10; whereas, if the gene frequencies had been 0.99, we would have had 1:1.1 chances. That is, if a herd was almost all *AA* with very few *Aa* or *aa*, *BB*, with very few *Bb* or *bb*, *CC* with very few *Cc* or *cc*, etc., it would not be difficult to keep them *AA*, *BB*, *CC*, etc.

It is obvious that increasing the number of gene pairs being selected for reduces the chances of securing them all in a homozygous state. If we increase the pairs to 10 and leave the frequency at 0.99, our chance of success drops to 1:1.2, whereas increasing gene pairs to 20 reduces our chance to 1:1.5, and increasing the gene pairs to 50 reduces our chance of success to about 1:3. In practice the more things we try to select for simultaneously, the more likely we are to fail. In our college dairy herds, we feel that we must have both good type and good production. The genes, however, that bring about style, straight tops, fine withers, well-set legs, etc., do not necessarily have anything to do with the physiological functioning of the organs and glands that result in a heavy milk flow. If we could select for production alone, we probably could get it more quickly, and we might end up with animals which were of less-than-average merit in type, though this is not necessarily inevitable. If one-third of the animals in any dairy breed would suit us from a production standpoint and one-third of them from a type standpoint and these two things were not closely correlated, then it is obvious that only one-ninth of the animals of the breed would suit us from a combined standpoint of type and production. The more uncorrelated things we select for simultaneously, the more we narrow our range of selection and the more we reduce our chances of success.

It is apparent that it would be easier to find an animal having at least one of the desired genes than it would to find one having both, since, if q^2 are *AA* and $2q(1 - q)$ are *Aa*, then those which have at least one *A* are $q^2 + 2q(1 - q)$, or $2q - q^2$, which may be written $q(2 - q)$. This can also be extended to n pairs of genes by applying the formula $[q(2 - q)]^n$. Thus, in our last example of a dihybrid with equal gene frequencies, we would have $[q(2 - q)]^n = [0.5(1.5)]^2 = 0.75^2 = 56.25\%$, or 1:2 chances of getting an animal that had at least one *A* and one *B*. With q at 0.4 and five pairs of genes, $[q(2 - q)]^n = 10$ per cent, so we would have 1:about 10 chances of getting an animal with at least one dominant gene in all the five pairs involved; whereas, if the gene frequencies had been 0.6 for each of the five pairs, our chance would have been 1:2.5; at 0.8, it would have been 1:1.2; at 0.99, it would have been 1:1.001, or a practical certainty. Lowering the gene frequencies or

increasing the number of pairs of genes involved curtails the likelihood of selection being successful.

From the above discussion and in view of the fact that most of our animals are still relatively heterozygous (gene frequencies around 0.5) for many pairs of genes and that most of the commercially desirable qualities are probably controlled by many (perhaps 20 or 100) pairs of genes, the breeder's task is seen to be very difficult and complicated. With intelligent selection, however, based on recorded data, he can favorably influence gene frequencies in his herd or flock. He may never render his animals homozygous for all the desirable genes, but he has the assurance that the merit and value of his animals will increase with the increasing frequency of desirable genes.

It is obvious also that selection for a recessive is much more simple than selection for a dominant owing to the fact that, if dominance prevails, then *AA* and *Aa* animals are indistinguishable phenotypically, while the *aa* animals can be recognized genetically from their phenotype. The Suffolk horse is a good example of this, its color, chestnut or sorrel, being due to a pair of recessive genes, this being the only color found in the breed. If early importers and breeders of Holsteins had elected the red and white instead of the black-and-white color pattern, they would not have been plagued with off colors that often lead to suspicion of the purity of breeding of the animals producing them. When a red calf is born in a Holstein herd, the sire and the dam are, of course, jointly and equally responsible, each having transmitted the recessive gene. With 1 calf in 100 born red, the genetic make-up of the breed is 81 per cent *BB*, 18 per cent *Bb*, 1 per cent *bb* (red).

Just to weed out the reds as they are born will have little effect on purifying the breed for color, since 90 per cent of the *b* genes are hidden in *Bb* animals, while only 10 per cent are visible in *bb* animals. If we started with an F_2 generation that was 25 per cent *BB*, 50 per cent *Bb*, and 25 per cent *bb*, it would take eight generations of eliminating *bb* individuals to get the proportion down to 1 per cent *bb* animals, or 1:100; whereas to halve this amount, *i.e.*, make it 1:200, would require four more generations; to get it to 1:400 would require six more generations; and to get it to 1:800 would require eight more generations. This sort of mass or phenotypic selection is seen to work very slowly. It can be greatly hastened, of course, by discarding any animals that have offspring showing the undesirable recessive character and also those whose sibs, cousins, or other collateral relatives show the character, in other words, by adding genotypic selection to the phenotypic.

Most of the problems and examples used to illustrate genetic principles involve a very few sets of alleles. The student and breeder needs,

therefore, to remind himself constantly that this is, in general, an oversimplification. It is known, for instance, in the pomace fly, *Drosophila melanogaster*, that upwards of 40 genes function in producing the wild-type eye color of red. If 40 of these pairs were the necessary dominant genes but the forty-first pair had mutated to, say, garnet, then the eyes would be garnet instead of red. Some of these 40-odd pairs of genes are located in each of the 4 pairs of chromosomes.

In our domestic animals, there seem to be 20 to 30 pairs of chromosomes with perhaps 100 or more genes in each chromosome. What we are actually dealing with, therefore, from a practical standpoint, would seem to be a complex gene complex. We talk about individual genes, but we are actually dealing with blocks or groups of genes. It may be possible too that in a certain gene complex, the homozygous dominant AA serves best, while in another perhaps Aa does, and in still another perhaps the homozygous recessive is best. As we have said previously, the breeder is attempting by selection to put together the best possible gene complex, to influence the proportion of desirable genes in his stock in a favorable manner, and he uses a variety of criteria to measure the value of the gene complexes that he has or desires to get.

Gene frequencies for various qualities are quite variable both in and between various breeds. To take an extreme example, the genes making for the type and temperament associated with speed are very scarce in the Percheron breed of horses. Nevertheless, there are probably enough of them present so that many generations of selection for these genes would make them sufficient in number to produce a horse of considerable speed. Similarly, the genes for red color are very few in the Angus breed, but constant selection for them would result in changing the breed from black to red. And in Holstein cattle the genes for higher butterfat test (4 to 5 per cent) are relatively scarce, but enough of them exist so that selection over many generations could result in an average test for the breed of over 4 per cent.

If gene A is homozygous in a breed AA, then one mating is as good as another. If gene B is heterozygous, Bb, then best mating is $BB \times BB$; next best, $BB \times Bb$; and poorest, $Bb \times Bb$. If we start with $Bb \times Bb$, we have a ratio of $1B{:}1b$ gene. Now, if we cull the double recessives, in the next generation we have $2B{:}1b$; in the next, $3B{:}1b$, etc., according to the formula $(n-1)^2\,AA{:}2(n-1)\,Aa{:}1\,aa$. In the second generation we cull 25 per cent as aa; in the fifth generation, 4 per cent; in the tenth generation, 1 per cent under the formula $100/n^2$, but even here there still will remain 18 per cent as heterozygotes. Selection can and does change the relative frequency of genes, but it is very slow when selecting for a dominant gene and unable to fix the heterozygous con-

dition, as, for example, the roan color in Shorthorns or the blue in Andalusian fowl.

Heredity vs. Environment in Selection.—The past has seen many arguments between the hereditarians and the environmentalists, with first one and then the other having seemingly the better of the argument. The debate has of late tended to be resolved by the simple but far-reaching expedient of substituting *and* for *vs*. In other words it is not a case of whether heredity or environment is the most important. Both are important, one just as much as the other. Neither good genes and a poor environment nor bad genes and a good environment will give us a profitable and satisfactory animal husbandry. We must have both.

There is still a considerable problem in this field, not the old one of attempting to determine which is the most important, but rather that of perfecting devices that will measure the influence of the two in a given case. Obviously some characters, like color pattern, are largely hereditary, owing to the genes. Others, like milk in the pail or fat on the carcass, are determined both by the genes and their various interactions and by environmental factors—feed, care, etc.

The breeder's task is to determine to the best of his ability how much of the variance in any given case is due to environment and to make due allowance for it in practicing selection. This is necessary because, as we have already learned, only the hereditary variations are capable of being passed along to an animal's progeny. If a group of heifers in comparison with their dams had better feed and care, calved at a more advantageous season of the year, were better fed while milking, were not bred so soon after freshening, etc., with the result that they considerably exceeded their dams' production, it would obviously be unfair to attribute all this excellence to their heredity. Better or worse feed, weather, and other environmental conditions could make a considerable difference in a crop of lambs or pigs, even though there were no appreciable genetic differences.

At present, the breeder has no practical tools for separating the genetic from the environmental causes of variation except his own judgment applied to individual cases, and his judgment unsupported by factual material in the form of carefully kept records is liable to be untrustworthy. If he will keep records, however, and appraise them intelligently and fairly, not letting his judgment be warped by individual likes and dislikes in regard to his breeding animals, he will be well on the way to avoiding the all-too-common mistake of assigning to heredity what rightfully belongs to environment. His success or failure depends to a large extent on his ability to do just this, for the simple reason that

hereditary differences may be transmitted, whereas environmental ones apparently cannot be transmitted.

In nature the gene complexes which would yield the best result in the given environment were the ones which eventually won out in the ruthless battle for survival and perpetuation of the species. The environment probably did not cause the original variations, but crossing, recombinations, crossings over, mutations, and chromosomal aberrations did. The germ plasm provided the base for variation and the environment acted as a screening agency.

In practical animal breeding or animal production, the environment is of equal importance with heredity. "Half the breeding goes down the throat." If we are going to measure differences in heredity, the environment for different animals or groups must be as constant as possible. Likewise, if we attempt to measure differences in environment, we must do it with animals which are as alike as possible genetically—inbred lines. There are many examples in animal-husbandry literature of purebred animals which have been selected to perform well under certain environmental conditions failing dismally when taken to some different environment for crossing with native animals. Khishin,[1] for example, reports the failure of dairy Shorthorns to hold their own production for more than one or two lactations in Egypt and to cross successfully with native cattle beyond the F_1. Dairy breeds with high inheritance for milk production have quite generally failed in crosses in tropical countries. Various admixtures of Brahman cattle with European beef breeds have, on the other hand, been successful in establishing more successful lines or breeds for tropical or semitropical conditions.

Animals should be selected and tested under conditions similar to those in which they are to be expected to perform. If the regime is to be three-times-a-day-milking, cattle should be tested under those conditions. Cattle which do best under a two-times regime will not necessarily do best under a three-time system and vice versa.

Optimum conditions for performance should be provided. Two or more groups of animals may gain at about the same rate under limited feeding thus making them appear phenotypically the same. When placed on full feed, however, there may be marked differences in their ability to consume feed and to utilize it for growth. If we expect a certain quality to manifest itself, we must provide the maximum opportunity for this to happen.

The Market and Selection.—The ultimate purpose for which animals are bred is that of supplying the needs and desires of consumers. The

[1] Khishin, A. E. F., Twenty Years of Shorthorn Feeding in Egypt, *Empire Jour. of Expt. Agr.* Vol. 17, No. 66, 1949.

market pays more for a low-set, blocky, well-finished, and marbled steer than it does for an upstanding, narrow animal in thin condition, because the former satisfies the wants of the consumer to a greater degree. Horses of accepted draft type and cows of dairy type will command higher prices than animals lacking these outward appearances, because the buyer feels that they are better equipped to perform their respective functions. The breeder, therefore, should be a careful student of market demands. Coupled with this should be a careful scrutinizing of his records in order to ascertain the type of animals that actually returns the greatest profit to the breeder, because the animal that brings the most money on the market is not necessarily and always the one that nets the breeder the most profit.

Most breeders must make their living through selling the animals they breed or the products therefrom. The mere fact that they have produced efficient and attractive animals will not of itself prove profitable if the market does not happen to be in the mood to buy that particular sort of animal or product. The breeder who is to get ahead must be a keen student of what the market demands and is apt to demand in the next few years. This should not, in the slightest degree, be construed to mean that breeders should follow every whim of the market and be continually attempting to change type. Such practice can lead to nothing but chaos. The successful breeder is the one who can sense the difference between a passing whim and a permanent change. The market is not a fixed institution incapable of change. For substantiation of this, one need but refer to pictures of accepted animal types of 20 years ago and to consult market statistics of two decades past. The progressive breeder senses each change somewhere near its beginning and shapes his course accordingly. In so doing he begins to practice selection for the new type one or a few generations before his fellow breeders and generally reaps a financial reward for his shrewdness and foresight. He also, of course, runs the risk of guessing wrongly—for which he probably will pay a penalty.

What type changes in draft horses will be expedient or necessary in view of the increasing use of tractors? What type changes would be desirable in dairy cattle owing to the likelihood that we will want to feed them an increased (or decreased) proportion of roughage? Will a changing feed situation, new knowledge of the functions of the endocrine glands in growth and fattening, or possible adjustments in our system of governing ourselves make somewhat different types of meat animals desirable? "Ty" Cobb was a great baseball player because he had the imagination to outguess the opposition plus the skill to carry out his plans. He is a great general who outguesses the enemy, a great lawyer

who outguesses his adversary in the courtroom, a great scientist who outguesses "nature." Outguessing simply means that the person had curiosity or imagination or vision. For real success the livestock breeder needs more than a sprinkling of this ingredient. Before turning his

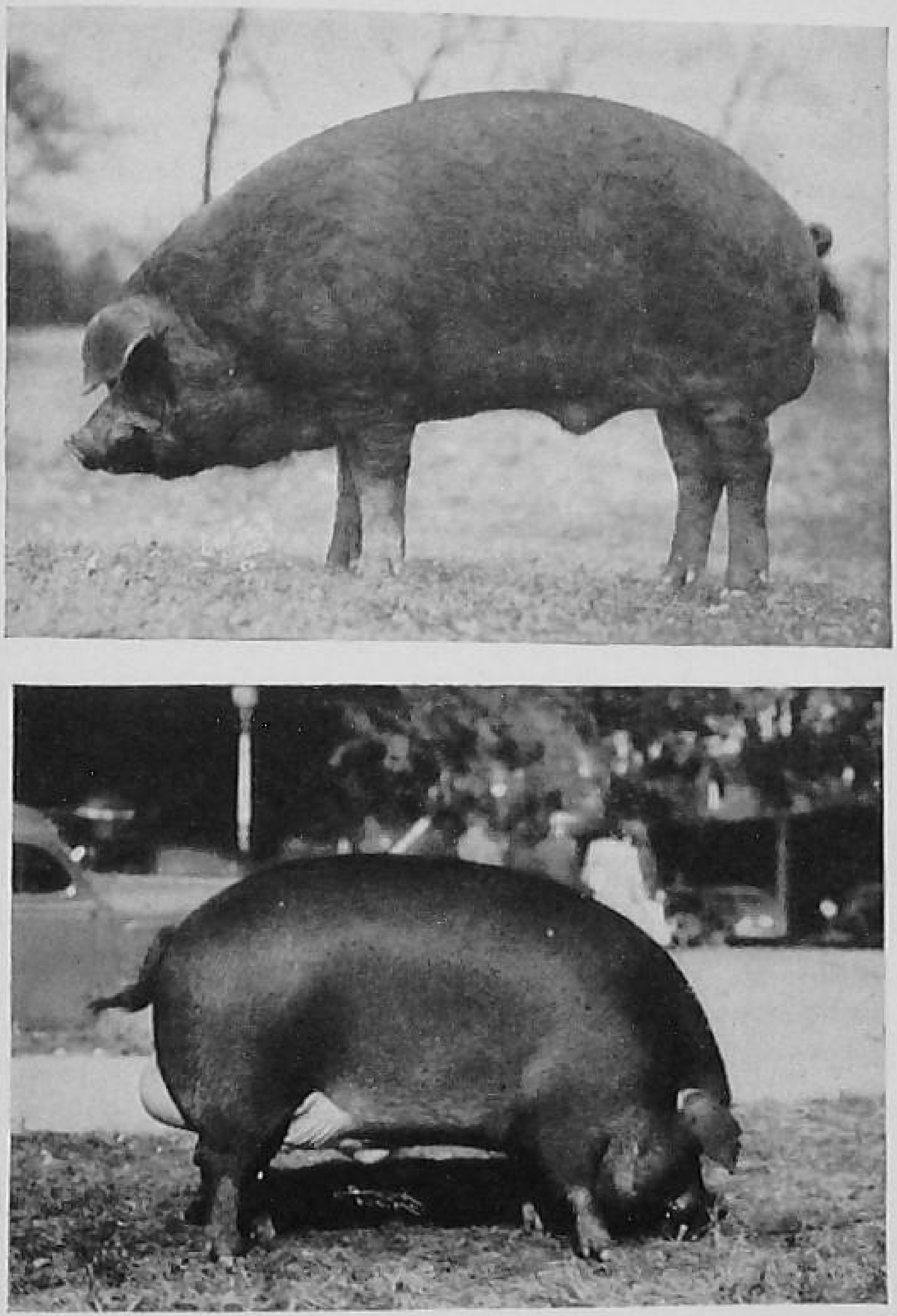

FIG. 167.—Grand Champion Durocs showing how ideals of type change. Above, Wavemaster Stilts, 1931 Grand Champion; and, below, Top Set, first aged boar, Iowa, 1947. (*Courtesy of Duroc Record Association.*)

hand to produce anything, every breeder and farmer should reflect on this most important of all questions, what will the market pay me best to produce? Until that question has been answered, there can be no consistent selection.

Breeds and Selection.—That there are differences between our pure breeds of horses, cattle, sheep, and swine needs no particular elaboration

at this point, for they are obvious. They arose because breeders have followed somewhat different ideals in practicing selection over a period of time and were able to influence the frequencies of certain genes in a recognizable fashion.

There are wide differences both between breeds and between individuals of a given breed. Breed differences may be due to the fact that breed 1 is generally *AA*, whereas breed 2 is generally *aa*. Such differences do actually exist, but they are not now thought to be so important as formerly. Another way in which breeds differ concerns the relative frequency of a given gene within the two breeds. Breed 1 may be 90 per cent *A* and 10 per cent *a*, whereas another breed may be just the reverse. The genes for high-butterfat test are much more prevalent in Jerseys and Guernseys than they are in Holsteins. This is due largely to selection. Holstein breeders for many years based their selection largely on amount of milk. It is well known that there is a negative correlation between amount of milk and its butterfat percentage. In other words, in selecting for high milk, Holstein breeders automatically rejected the genes for higher test, so that the Holstein breed now produces a milk with about 3.5 per cent butterfat, whereas Guernsey milk averages about 5 per cent and Jersey milk about 5.4 per cent butterfat. The relative scarceness of the genes for higher test in Holsteins makes the job of developing a 4 per cent herd very difficult. If a breed totally lacked the genes for some desired character, then there would be no other recourse but to go outside the breed to get these desired genes.

There is nothing in the mechanism of inheritance itself that will change the frequency of any gene in a breed or population. If we start with two animals that are *Aa* (one-half the genes *A* and one-half, *a*) and do not select for gene *A* or gene *a*, then after any number of generations and with any system of breeding, there will still be as many *A* genes as *a* genes in the population. It must be recognized, however, that chance may lead to rather large fluctuations in gene frequencies in small populations.

A stock phrase for many years has been, "There is no best breed," though this statement is only true when there has been added, "for all conditions." There are breeds better suited to certain conditions than are others of the same class, because certain breeds have been grown under, and with a view to fulfilling, similar conditions to the ones now contemplated. Some of our breeds of dairy cattle produce a milk better suited to cheese making or the production of evaporated or condensed milk than do others. Comparable situations exist between breeds of horses, sheep, and swine. Breed tests of various sorts are likely to be very misleading, because in them it is more apt to be the particular strain

rather than the breed as a whole that is being tested. If enough so-called "breed tests" were run, under a wide enough range of environments, no doubt all the breeds would get a share of the winnings. A breeder will find it profitable to make a study of the breeds in order to ascertain which one has been produced under conditions similar to his own and has given the most general satisfaction therein. On the other hand, caution must be exercised in accepting the offerings of overenthusiastic breed advocates. This matter of an unbiased opinion and a thorough knowledge of the breed from its earliest inception to the last sale and showyard winning or loss cannot be overstressed. Such knowledge is essential before a pedigree in the breed can be properly evaluated.

Each of the breeds has certain exterior trade-marks that make it possible to differentiate the breeds without any serious likelihood of error. In this sense the trade-marks are an advantage. They may also, of course, be a disadvantage if breeders select for fancy points at the expense of points of utility. In sheep, one breed calls for a long, horizontal ear, others for short, horizontal ears, and others for an erect ear; some breeds demand a very heavy face covering of wool, others a moderate face covering, and still others a clean face; some demand the color markings on face, ears, and lower legs to be black, others brown, others gray, others white; some breeds have no horns, others horns in the male only, others in both sexes.

In swine, some breeds demand erect ears, others moderately erect ears, others lop ears; in some the face must be greatly dished, in others moderately dished, in others straight; some are black colored with a slight toleration for white, others white with a complete intoleration for black, others varying shades of red, and one requires a white belt to include the front legs and shoulder. The dairy and beef breeds also vary in color, horns, face. The most acceptable colors of Percheron horses, grays and blacks, are not acceptable in Belgians; and the ones the Percherons frown upon, chestnut, sorrel, bay, and roan, are the desired colors in Belgians.

The breeds should continually scrutinize these trade-marks. Most of them in themselves are harmless, although some may have positive detriment, horns, face coverings, etc. Reasonable trade-marks should be maintained, but care must be exercised at all times that "the tail does not get to wagging the dog." The principal advantage of the trade-marks is not that they have any intrinsic merit in themselves but that they do enhance uniformity of appearance, and their very existence and recognition reduces the likelihood of fraudulent or careless registration and so helps to protect the purity of the breeds. The existence of separate and distinct breeds has two very important functions; (1) in

encouraging cooperative effort among men in the same breed, and (2) in stimulating competition among the breeds.

Trade-marks generally mean some compromise in selection. The breeder has to get a little less of some intrinsically valuable trait because he has to get more of some breed trade-mark. Breed score cards generally try to allot point scores on the basis of relative merit of the part or trait considered. Breeders should use this technique in practicing selection so as to strike the happy medium between paying no attention to breed trade-marks and paying them too much attention.

In the choosing of a breed, one must reach a decision as to whether to select a breed already numerous and well established in the region or to introduce a new and unknown one. Both of these procedures have advantages and disadvantages. If a new breed is chosen, one has the advantage of novelty and monopoly but the very serious disadvantage of standing alone and perhaps being far removed from other sources of replacement. Conversely, if one chooses a breed that is prominent in the locality, he can have the distinct advantage of other breeders' experience with the breed and the opportunity of wide choice near at hand for his foundation animals and later additions. The good and bad features of other herds in the community are more or less generally known as well as the integrity and dependability of the men themselves.

With the growing trend toward the proving of sires in all classes of livestock, the exchange of good sires in a region in order to extend their use over longer periods of time will probably ensue. Having animals of the same breed as others in the region would allow a new breeder to take advantage of opportunities of this sort. General adoption of such a plan would also tend to create linebred herds in the district, something greatly to be desired in American livestock breeding.

Likewise, the trend toward artificial insemination in some classes of livestock would indicate the much greater likelihood of one's being able to have the use of better sires if he were breeding animals in a breed already numerous in a region.

Finally, the greater likelihood of developing a market that would attract outside buyers and permit the fostering of consignment sales is an advantage which can grow out of a community's sticking to one breed. Choosing a breed already well established in a region seems to hold more advantages to the newcomer than the alternative scheme of choosing a breed with few or no breeders in the region.

Individuality and Selection.—What an individual is and does is called its phenotype, so that selection based on individuality can properly be called phenotypic selection. This has been the most commonly used tool in selection, and to it can be ascribed most of the progress that has been

made in shaping nature's imperfect offerings into more efficient and desirable types. Now that the physical mechanism of inheritance is known, we can, of course, better appreciate the shortcomings of phenotypic selection. Breeders used to think (and some still do) that they could tell from the appearance (phenotype) of an animal just how it would breed. The informed breeder now knows better than this. He knows that he may learn certain things about probable transmitting worth from appearances, that he can add to his knowledge from a pedigree which is relatively complete with phenotypes of the ancestors and collateral relatives and their offspring, but that actually to ascertain the breeding merit of any animal, he must study the animal's offspring, in other words, apply the progeny-performance test.

All these considerations are important, though there can be no question but that, ideally, the progeny-performance test takes first rank. A good individual and a good pedigree are obviously considerations of great importance. A deficiency in either individual or pedigree is, of course, to be avoided wherever possible. Selection based on individuality alone or on pedigree alone or both, however, will involve only temporary loss and setback, provided the progeny-performance test is rigorously applied. A thorough study of its physical make-up is essential in selecting an individual to go into the breeding herd. It is here that knowledge of anatomy and practice in judging livestock will stand the breeder in good stead. There can be no question but that livestock shows are very influential factors in establishing type, and breeders generally would profit by more regular attendance at the leading livestock shows. It should be remarked however, that show standards for various breeds and judges' interpretations of them are not necessarily infallible. As an instance, we need but mention face covering in certain breeds of sheep—demanded by show-ring standards but now thought to be anything but advantageous from a practical production standpoint. Like other arts, livestock judging is more or less a gift, but it too can be improved through study and practice. The animals that go to make up a herd should be as nearly perfect as possible, but in all animals it is possible to find faults of various sorts. This being true, wise selection will depend on the breeder's ability to balance one fault, or several faults, against others and to choose the lesser of the evils.

In selecting foundation animals, it is essential that there be as much uniformity as possible in the band of females. If these are of different types, it will be extremely difficult to get a sire which, when mated with them, will be able to produce a uniform type of offspring. In visiting herds or sales for the purpose of securing foundation animals, one of the cardinal features to be observed and appraised is this matter of uni-

formity. Uniformity of a good sort is a virtue almost beyond price. One should hesitate, if not entirely refrain, from buying animals out of a flock or herd that evidences samples of all conceivable types. The females, besides being uniform in type, should be of good size in order to facilitate prolificacy and to promote efficiency. The desideratum is as much size as is consistent with quality. Size, however, as well as anything else, can be overdone. If the females of any class of livestock are not fairly roomy and stretchy through the middle, the most important feature of all in breeding livestock, *viz.*, fecundity, is apt to be low.

In selecting the sire to mate with a uniform band of good-sized females, the cardinal point to be borne in mind is that he should offset any faults that are present in the females. If the females have a tendency to sloping rumps, the male should be particularly strong and level in this respect, as well as being a member of a family strong in this regard; if they show weak pasterns, he must stand well up on his toes, etc. If size and vigor are present in the females, one can logically accept a little more compactness and quality in the male, especially if producing meat animals. In the sire, there should be evidence of masculinity, but it should be remembered that this is often overdone at the expense of quality. Breed history, both good and bad, must also be considered. Particularly is it essential in selecting animals of any breed to avoid those individuals exhibiting the common breed faults, such as droopy rumps, small teats, etc., in some of the dairy breeds, too fine or too coarse bone in some breeds of horses, undue coarseness in some of the breeds of swine, etc., through all our classes of livestock.

Many breeders base their selection almost wholly upon individuality. This procedure, however, is not genetically sound, for the reason, explained earlier in this chapter, that variation, or variance, is caused by dominance, epistasis, and the environment, as well as by genes acting additively. Most experiments show that the latter kind of variation makes up only one-tenth to one-third of the total variation. This does not mean that we should make no effort to capture this type of variation. Fast horses do not always beget fast offspring, but they are more likely to than are slow horses, and so on for other qualities in other classes of livestock. Phenotype and genotype are not necessarily identities, but phenotype is a worth-while indicator of genotype. Phenotype is determined both by genes working in a variety of ways and by an unimaginably large number of environmental effects. Certain, but not all, gene effects will be transmitted. No environmental effects will be. We cannot even tell by inspection whether a black bovine is *BB* or *Bb*. In either case it will be black; *i.e.*, these two genotypes belong to the black phenotype. From a breeding standpoint, however, these two animals are very differ-

ent, for they belong to two different genotypes. When mated to red cattle, the first, *BB*, will give all black offspring, whereas the second will give 50 per cent black and 50 per cent red offspring. This is a simple case, to be sure, involving only one pair of genes, but the same reasoning and the same or more complicated genetic principles apply to the more complex characteristics, such as speed, milk production, ability to fatten, plus the much greater range of environmental effects. It is all right to demand high individual excellence in selecting breeding animals, but it is all wrong to stop with that single consideration.

Dairy-cattle breeders have, to some extent, aped the breeders of fat stock and horses and set up arbitrary standards of dairy type. There is a great difference, however, between the selection of beef cattle, for example, and dairy cattle. In the one case we deal with tangibles and in the other largely with intangibles. The beef animal, male and female, exhibits directly the presence or absence of the desired qualities, *e.g.*, degree of fleshing, width of loin, fullness of round, etc. With dairy cattle, on the other hand, there seems to be little correlation between type and production in the female, and, of course, the bull gives no milk whatsoever. On the face of it, it would seem to be a very naïve assumption that straightness of topline or stylish carriage, for instance, could have any direct bearing on the amount of milk which a cow could give.

It is extremely difficult to tell by looking at a dairy cow how much milk she is capable of yielding. Many of these so-called "guessing contests" have been staged. One was held at the New York State Fair in 1919 which included nine cows ranging in production from 4,454 to 20,852 lb. of milk a year, with about a 2,000-lb. interval between each pair. Over 70,000 people guessed, no one got over five of the cows properly arranged, and only 12 people did this well, one-third of the guesses failed to have even one cow in the proper place, and many "guessers" picked the lowest producing cow as the highest producer. So, if it is hard to estimate individual performance by inspection, how futile and hopeless appears the task of estimating transmitting abilities by inspection.

Individual selection can be practiced in terms of individual characters, groups of characters, or in terms of general average excellence. In hogs we might decide to cull all animals with weak pasterns or those with steeply sloping rumps or those with heavy jowls or perhaps those with all three deficiencies. In doing so, we might be throwing away many genes for high fertility, for high proportion of valuable cuts, for large milking ability, etc. Likewise in keeping the good pasterns, rumps, or light jowls, we might also be keeping low fertility, poor quality, lack of

ability to raise pigs, etc. If selection were practiced on the basis of general average excellence, we would perhaps keep some sows with poor pasterns, steep rumps, and heavy jowls because they had enough other good qualities to give them an average score that was higher than other sows which might excel in some specific characters. Similar illustrations can be envisioned in all classes of livestock. It is often noted with a beginning class in livestock judging that as specific animal faults are pointed out, each one in turn tends to bulk too large in the beginning student's mind, so that an otherwise excellent animal which exhibits this particular fault is dropped clear to the bottom of the class. Some students find it impossible to overcome this tendency. Improvement in livestock judging on the part of other students is merely the growth in ability to balance defects or imperfections and arrive at a sound judgment based on the total average excellence of the animals in each judging ring. The good judge sees all the good and the poor points of his animals but makes his placing on the basis of general balance of all parts. The good breeder practicing phenotypic selection does the same thing in his own "Little National or International" that he holds in his own barnyard.

The shortcomings or selection based on individuality can best be illustrated by calling to mind excellent individuals in fat-stock classes or horses that have failed to transmit their own good qualities to their offspring. There have probably been many animals that stood at or near the top in the show ring and at the same time were mediocre or worse as breeders. Likewise, some animals that stood lower in their show classes, or perhaps were never deemed worthy of showing, have proved to be excellent transmitters of desirable type.

Another more general critique of the limitation of selection based on individuality is the very slow pace of the rise in production in dairy cattle. For many years dairymen have saved heifers from the highest producing females and sons from their highest producing cow. Yet the average cow now yields 5,000 lb. of milk and 200 lb. of butterfat.

For qualities which are highly hereditary, individual selection is the simplest and most useful tool we have. Its main limitation arises from the fact that heritability of the commercially valuable qualities is relatively low. It is a general principle that the longer we can delay selection, the fewer mistakes we are likely to make. If we selected ewe lambs the day they were born, many mistakes would be made; if we delay until they are yearlings, fewer mistakes would result; if we could try them all out for 4 or 5 years and then select on the basis of individuality and progeny, relatively few mistakes need be registered. So another limitation of individual selection lies in the fact that it is based on young and untested judgments.

Pedigree and Selection.—It might perhaps seem logical to expect the individuality of an animal to mirror fairly exactly its transmitting ability, but such an expectation comes far from being 100 per cent fulfilled. Likewise, it might seem logical for a pedigree to predict breeding worth with considerable accuracy. If the expectation is built upon pedigree phenotypes, it will fail for the same reason that individuality fails as a prognosticator. Actually, the pedigree is often used not even as a group of phenotypes, but only as a group of names, the estimator actually knowing little or nothing about the animals represented by the names. In such a situation pedigree study probably hurts more than it helps. Many new breeders, after reading nothing more basic than breed magazines for a few months, consider themselves experts at predicting future breeding worth of young animals after a séance with the names in their pedigrees. Perhaps this partially explains the rapid rate of turnover in this class of breeders.

Pedigrees have limitations as selection indexes. The first one is perhaps the fact that a pedigree is a selected group of animals. In a hog's pedigree, his sire may be one of 100 sons of the paternal grandsire and one of 25 sons of the paternal granddam. In cattle the sire may be 1 out of 200 sons of the paternal grandsire and 1 out of 3 or 4 sons of the paternal granddam. The sire in any pedigree has a whole host of possible paternal and maternal half brothers and sisters, uncles and aunts of the animal whose pedigree we are considering and their offspring cousins to the pedigreed animal. The sire in any pedigree may have a lot of other offspring, half brothers and sisters to the animal whose pedigree we are considering and their offspring nieces and nephews to the pedigreed animal. Likewise, for the dam, grandparents, etc. A pedigree is a tiny, selected sample of a whole host of animals, the whole being the immediate family of the animal. If you were shown a picture of a first-floor door, two second-floor windows, and four third-floor clapboards, could you very accurately visualize what the whole house looked like? That's about how difficult it is to arrive at a reasonable judgment of the probable genotype of an animal from its direct ancestors, its pedigree.

Not only are the direct ancestors a selected group, but the printed catalogue material about them is also often of a selected nature. A bull has 40 tested daughters and the records of the top 5 are listed. A cow has six records and only the best one is listed. In many fat-stock pedigrees nothing is given except the animals' names. So pedigrees are lame as selection tools because the animals and their accomplishments are both selected. If one had a barrel of apples of which a few were sound and the rest in varying stages of decay—some being completely rotten—one would get a distorted notion of the whole barrel if he based

his judgment on someone's picking out 20 apparently sound apples and then sorting them down to 10 by throwing out those whose rottenness was underneath and did not show up when the choice of 20 from the barrel was made.

As presently used, pedigrees are not very useful tools in selection. They can be improved in a variety of ways. The most obvious way is to print all the known facts about each animal as an individual, *i.e.*, give as complete a phenotypic picture of each animal as possible. Next include as many of the close relatives as possible, uncles, aunts, cousins, nieces, nephews. True, an animal gets no inheritance directly from an aunt, but an aunt is 12.5 to 25 per cent related to the animal in question. The more close relatives we can see and whose records we can study, the more reasonable judgment we can make regarding probable genetic worth of an untested animal. Collateral relatives' and direct ancestors' accomplishments can be evaluated in terms of the degree of relationship existing in each case.

The earliest pedigrees were not written in the present-day bracket form. Instead, the animal's name was set down, and over to the right on the same line was listed its sire (and still further to the right the breeder of the sire). Underneath the animal's name appeared that of her dam and out to the right of the dam was listed her sire and her sire's breeder. In other words, the left-hand column, as you read down, gave the animal, his or her dam, his or her maternal granddam, his or her maternal great-granddam, and so on, and the next column to the right gave the sire of each of these cows. The first way of writing pedigrees, therefore, gave just the bottom line of the pedigree. In the schematic pedigree shown as Fig. 168, animals below the diagonal line would appear in the old-style pedigree; those above the diagonal line would not appear.

We think that the old-style pedigree, properly used, has several advantages over the present-day bracket form of pedigree. We do not expect breeders to go back to the old-style pedigree—there is no need to, since the old-style pedigree is included in the bracket style anyhow (it is the bottom line).

What we mean by using the old-style pedigree properly now needs some discussion. Let's start with sire A in Fig. 168. We are assuming that this is a good proved sire. Since not too much can be told from the type of a bull about how his daughters will produce or look and because of the shortcomings of pedigrees as production-prediction tools, it makes it necessary that sire A be a proved sire if we are really to know about his transmitting abilities.

If sire A is a good proved sire, that means that good stuff has come out of him. Now, if good stuff has come out of him, it is very certain that

good stuff must have gone into him from his parents—if it had not gone into him, it could not have come out. If, on the other hand, sire A is a poor proved sire—poor stuff has come out of him—then it makes no difference how good his pedigree seems to look (or even actually is). If there was good stuff in A's pedigree, but A did not get it in the sperm from C and the egg from D, then A certainly cannot pass it on; he can only pass along sample halves of what he actually got from his parents. So, we repeat, let sire A be a proved sire, and whether proved good or proved poor, what is apparently in back of him in his pedigree cuts relatively little figure.

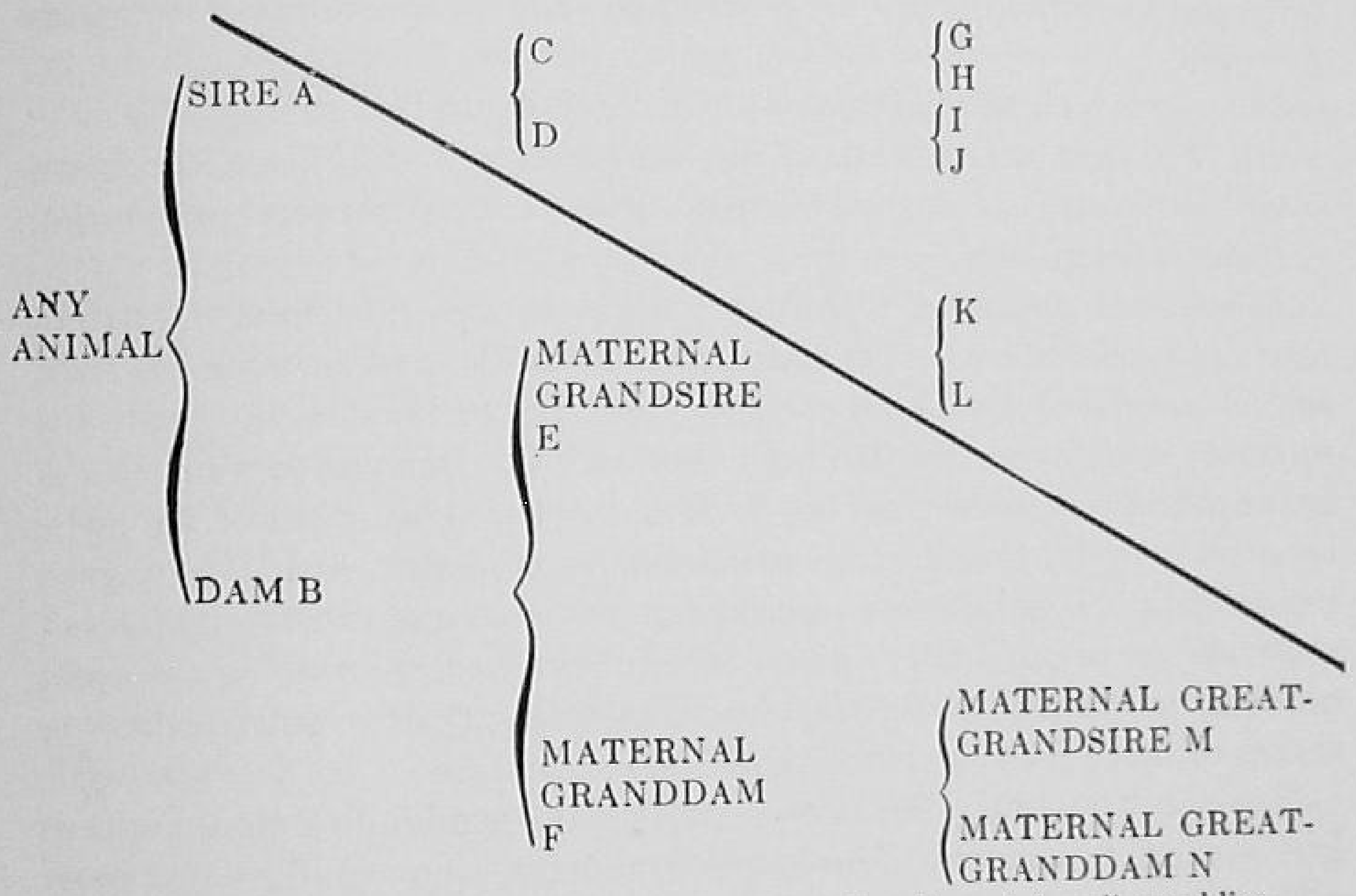

FIG. 168.—Schematic pedigree showing "old-style" pedigree below diagonal line.

(If, on the other hand, sire A is a young, unproved bull, then we have got to try to guess from his pedigree as to what he got and we would do it by the method we are describing.)

We would apply the same line of reasoning to maternal grandsire E (Fig. 168) as we have just applied to sire A. If grandsire E is a good proved sire, then what's back of him cuts relatively little figure.

And likewise for maternal great-grandsire M.

In short, if sire A—grandsire E—and great-grandsire M, are good proved sires, then we can forget about what's back of them—the material above the diagonal line in Fig. 168—and concentrate all our efforts and study on the material below the diagonal line.

This may sound a bit revolutionary, but actually it is not. When

we say that if sire A (and grandsire E and great-grandsire M) is a good proved sire, we can "forget what is back of him," we are not actually forgetting anything. If sire A is a good proved sire, there must have been good stuff in his ancestors—that is the only place from which he could have gotten it. But, if sire A is proved good, then the goodness behind him has been focused or brought together in him. When it is once brought together and proved in him, we know it is there and so need not go behind him to his ancestors. That is all we mean by saying that we can forget what is behind him. We do not actually forget what is behind him in his pedigree—we use it—but we use it where it is focused or brought together in sire A, rather than where it was diffused out in his pedigree.

Now, let's look at the female side of the bottom line of Fig. 168.

We will start with the dam B. As indicated earlier, we can learn something about how she will transmit from her own type and production records—we can learn something more perhaps from studying her pedigree—but the real proof of how she can transmit can come only from how she does transmit. In short, until dam B has had some records, and some offspring with records, we can't really know what kind of a producer and transmitter she actually is. We demanded that sire A be a good proved sire—likewise, if we want to take as much of the guess as possible out of breeding, we must also demand that dam B be a good proved cow. If dam B has transmitted well to a couple of daughters or sons (the more the better), there is a fairly good chance that she will continue to transmit well to her future offspring (half or full brothers or sisters to those she has already had).

We, of course, apply the same reasoning to granddam F that we have just applied to dam B. She is older and can and should have more offspring than dam B. Granddam F's other daughters or sons are, of course, aunts and uncles to the offspring of dam B, and any offspring of these aunts and uncles are cousins to the offspring of dam B.

The same line of reasoning applied to dam B and granddam F we will also apply to great-granddam N.

The trend toward printing all the offspring of the females on the bottom line of the bracket-type pedigree, together with their type and production accomplishments, is to be highly commended. All these animals taken together make up the female family, and when we have this data, we have a much wider and more secure foundation on which to base our judgment of probable genetic worth than we do when we have to base it on just dam and maternal granddam and great-granddam.

We like to think of this female bottom line of a pedigree as a stream which flows in Fig. 168 from great-granddam N to granddam F to dam

B, and finally to the present "Any Animal" being considered in Fig. 168. If great-granddam N is a great female herself, in type and production, and has had several good offspring, among them granddam F, and if F in turn has had several good offspring, among them dam B, and if B has had one or some good offspring, then we can be sure that the stream (which is actually the female family) is a good one.

Now if, in addition, great-grandsire M was a good proved sire and poured into the stream the hereditary determiners for good type, high production, disease resistance, regularity of breeding, longevity, and the other good things which we want in our herds, and if maternal grandsire E and sire A did the same thing—then the good maternal stream which we started with in great-granddam N will have had the best possible chance to become enriched as it flowed down the generations.

Many breeders seem to consider all the 14 animals in a three-generation, bracket-type pedigree as about of equal importance and to base their judgment largely on the individuality (type and/or production) of those 14 individuals. Such a procedure is good as far as it goes, but not so complete and efficient as it might be.

It would be much more efficient, we think, to work with only the six animals concerned in a three-generation, old-type pedigree—the bottom line, but to get all the information available about these animals. Study sire A thoroughly:

What kind of females was he bred to (production and type)?

What kind of offspring did he get?

Did the offspring and dams have similar environments (feeding, etc.)?

Has he any sons that are transmitting well?

Has he any full or half brothers or sisters which have done well?

Perhaps sire A has 30 daughters, 5 sons, and 30 or 40 paternal and maternal full or half brothers and sisters. So, instead of just studying sire A as an individual and learning about a few of his offspring, we should study carefully and completely not only sire A himself, but some 70 or 80 of his offspring and close relatives.

We would carry out similar studies on the other five animals—B, E, F, M, N, in Fig. 168. We are going to take the really functional part of a pedigree and study it as completely and exhaustively as possible. So, while we advocate discounting to a certain extent about half the animals in a bracket-type pedigree (those above the diagonal line in Fig. 168), we also advocate doubling or quadrupling the amount of study and thinking we give to those making up the bottom line of the pedigree.

The bottom line of the pedigree—the old-style pedigree—is really the "Functional Part of the Pedigree." When used intelligently, by getting all the relevant data possible, and in conjunction with selection for good

type and production in the females involved, we have the presently most valuable tool for arriving at the most probable transmitting values of our livestock.

Breeders have traditionally used three means to try to evaluate the transmitting abilities of their animals, and their availability to the breeder in point of time places them in the following order: (1) pedigree, (2) individuality, (3) actual breeding performance. When properly used, all these methods are useful in breeding better livestock, but they all have certain limitations. We can summarize by saying that, from the standpoint of hereditary transmission:

The pedigree of an animal tells us what the animal *ought to be.*

The individuality of an animal tells us what the animal *seems to be.*

The breeding performance of an animal tells us what the animal *actually is.*

Unjustified merit is sometimes assigned to any and all animals of certain strains or families. In common vernacular, this is known as a "pedigree craze." They are sometimes propagated for the sake of restricting competition, and the livestock breeder will do well to investigate thoroughly before shaping his course by them. Utility rather than popularity will, in the final analysis, be the criterion by which all classes, breeds, strains, and individuals will be tried. This should not be construed in any way to mean that certain strains or families are not better producers of speed, milk, flesh, wool, or what not, than are others, because such an interpretation would be entirely removed from the truth.

In planning matings, pedigree study has a legitimate place. Hard and fast rules cannot be laid down. It is a matter of reflection and judgment requiring intimate knowledge of the dominant characteristics of the strains in question. Some strains are too fine, others too coarse, some mature quickly, others slowly, butterfat percentage is high in some, low in others. To mate wisely, so that in all probability there will be blended in the offspring some of the extremes found in the parents is an art in the achieving of which pedigree study has its legitimate function.

It will readily be recognized that the number of animals in the most efficient strains is more or less limited. It is also a fact that because of their recognized merit there is a large demand for them, and they consequently sell for high prices. To the small breeder, this is discouraging, but he need not be without hope. These, to be sure, are proved strains, though, when their origin is studied, it is found that they arose more or less by chance through the mating of two particular individuals. Each parent probably supplied some previously missing factor or factors, which when combined into one individual yielded an animal of much greater worth than either parent and, moreover, an animal capable of

transmitting its own good qualities. It would be foolish to believe that what has occurred cannot be repeated. The small breeder with limited capital may, through a proper blending of strains, produce a strain more beautiful and more efficient than anything yet known. This does not mean that any breeder can be careless in selecting foundation stock or, in general, expect to get something from nothing. He should, by all means, select from proved strains as far as his finances will allow, because the isolation interpretation explains much more logically than does the mass-selection interpretation the progress that has been made in the past. When an outstandingly good animal arises from mating two more or less mediocre animals, the progeny-performance test must be very rigidly applied.

The greatest lack in animal breeding today is the lack of records. Until this deficiency is remedied, pedigrees will continue to be of relatively little use in enhancing the accuracy of selection. Attempts at remedying this situation are being made by some of the purebred breed associations by means of records of performance, but the problem is a very difficult one and a complete solution is not to be expected immediately.

Any individual breeder, however, is at liberty to set up his own system of record keeping at once, which greatly enhances his chance of successful selection in his own herd. Such systems of record keeping will be indicated for each of the classes of livestock in the next three chapters. Even when pedigrees can be made relatively complete from the standpoint of records, we must realize that we can probably never have a complete knowledge of the genetic make-up of any animal, and, even if we did, we would still have to face the sampling nature of the hereditary process, which would make it uncertain which member of each heterozygous pair of genes any individual actually received from its parents. Whether we gain more than we lose by culling a certain fairly good individual because of some fault in its pedigree is an unanswerable question. Again, as was said of judging or estimating individuality, we must try to strike a proper balance between individuality and pedigree.

The breeder's first concern will be to select good individuals. Complete pedigrees in terms of records of performance would be of inestimable benefit to him in deciding to keep one or another of two individuals of approximately equal merit. Complete pedigrees can be of great benefit also in arriving at an estimate of different female lines within a breeder's own herd. When pedigrees can be made relatively complete in terms of records of performance, one will also have considerable data on the collateral relatives of each individual, and, although it is difficult or impossible to assign definite numerical values to records of collateral relatives, they will, nevertheless, be very valuable in a general way.

Progeny Test and Selection.—The idea of progeny testing as an aid in selection has lately been revived and given much publicity. Like many other general ideas, this one is not new, having been advocated by a Roman, Varro, 2,000 years ago and having been used by Robert Bakewell in the eighteenth century in his practice of bull and ram letting. The progeny test finds its greatest usefulness with characteristics that can be expressed by only one sex, *e.g.*, milk or egg production, although there is no reason why it cannot be used to advantage with any class of livestock. Like any other selection device, this one has both advantages and disadvantages.

Owing to the relatively few offspring of most females, it cannot in general be applied to animals of this sex. Even with males their progeny-performance rating must come relatively late in their lives, after a sufficient number of their offspring have been born and reached such an age that their own performance has had time to be measured. Care must be exercised that excellences or deficiencies which are actually environmentally caused be not ascribed to inheritance in either the offspring or the parents. Allowance must be made for the fact that the females to which a male is bred are generally a somewhat selected group. It can thus happen that a breeder can be making progress, even though the total offspring of each of a series of males averages lower than their dams. We must not forget that the hereditary process is of a sampling nature, and we, therefore, will need enough comparisons to make reasonably sure that we have a fair sample of any male's inheritance.

Even with the above limitations, progeny testing is one of the keenest tools available to the breeder. It should be used to supplement individual and pedigree selection—not to totally displace them, as is sometimes advocated. The simplest type of progeny testing consists of the average record or merit of a sire's offspring. If the females to which two males are bred are an average of the breed as a whole, then such progeny records can be used to measure the breeding value of the two males concerned. If, however, the mates of one male were considerably above breed average, those of the other considerably below it, then such direct comparisons would not be justified.

Among the farm mammals, progeny testing has been used most with dairy cattle, a little with swine, and is just beginning to be used with the other classes. In dairy cattle, progeny testing has eventuated in several systems of indexing bulls for their level of transmitting ability for amount of milk and butterfat percentage. The system generally used can be illustrated by the following example. Suppose a bull is bred to 12 cows whose average production is 7,000 lb. of 3.8 per cent milk, and their daughters by this sire average 9,000 lb. of 4.0 per cent milk. Presumably

this bull has raised the production of his daughters by 2,000 lb. of milk and 0.2 per cent of butterfat. Because these qualities are apparently controlled by multiple genes, we assume that the sire and dam are jointly and equally responsible for the production of their daughters, in other words, that the daughters' production falls halfway between the two parental levels. Knowing the level of production of the cows and their daughters enables us to estimate the transmitting level of the bull.

	Pounds	Butterfat percentage
Dam's production	7,000	3.8
Daughter's production	9,000	4.0
Bull's index	11,000	4.2

It is obvious that before such figuring is justified, the records of both dams and daughters must be corrected to some standard basis. This is accomplished by means of various and sundry conversion factors. It is tacitly assumed that if the bull were sold to another breeder whose herd production also averaged 7,000 lb. of 3.8 per cent milk, the resulting daughters would also average 9,000 lb. of 4.0 per cent milk. This might or might not be the case, depending on many things but especially on the genetic make-up of the animals involved. Many different gene combinations might conceivably result in a production of 7,000 lb. of 3.8 per cent milk. Whether this proved bull would "nick" equally well, better, or worse in the second herd could only be ascertained by trying.

The U.S. Department of Agriculture Bureau of Dairy Industry proves bulls on the basis of 5 daughter-dam comparisons. Some investigators urge at least 6 comparisons, others 8 or 10. Obviously the error will be cut down as more daughter-dam comparisons are added, because the extreme variates will have a tendency to cancel each other, thus giving a truer average. If a breeder can successfully standardize his records—smooth out the environmental differences—and will test the first 6, 8, or 10 daughters as they are born in his herd without any selection, he will get about as good a genetic picture of his bull as he would with 30 or 40 daughters.

Attempts are now being made to work out comparable and practical systems of indexing males in the other classes of farm livestock. When available, such information should aid greatly in taking some of the "guess" out of breeding. And, even though most males cannot practically be indexed until after they are dead, the information can appear in pedigrees, which makes them of much greater value.

Probably the greatest advantage to the breeder from progeny testing

will arise from the records themselves rather than from their manipulation as indexes. When records are kept and intelligently studied, selection is bound to be benefited. Breeders too often depend on a somewhat unreliable memory and are prone to have favorites among their animals. Even a condemnatory record as a breeding animal at times fails to outweigh a breeder's fancy for some particular pet. Actually, of course, if one is not going to use the records, he is simply wasting his time in getting them. Progeny testing must be based on records, which, if carefully compiled and intelligently and, on occasion, ruthlessly used, can be the surest guide that a breeder can have.

Mass or phenotypic selection was practiced with poultry at the Maine Agricultural Experiment Station beginning in the year 1899. From this time until 1907, only those females were used as breeders that produced at least 160 eggs in their first year, only males whose mothers laid at least 200 eggs in their first year. Under this system of selection, the yearly egg production decreased steadily. The point to be noted here is that mass selection failed to increase production in the hereditary material involved. Whether this result was due entirely to the breeding system involved or in part due to unsuspected environmental changes, we do not know.

After 1907, the system of selection was changed. All females were now selected from high-producing mothers, the female progeny of which were all high producers, and, in case such a female failed to yield high-producing progeny the first year, she was not retained in the breeding flock. Males were selected from high-producing mothers whose female progeny were all high producers, and a male was discarded immediately if his progeny failed to be high producers. Pedigrees were also kept and proper attention was given to the blending of blood lines. With such a system in vogue, the production increased steadily from 1908 to 1920.

Mass selection alone in any given case might or might not yield successful results. In order to reduce the chance of failure, progeny testing needs also to be invoked. Certainly much of our livestock improvement has come about through the intensive use, often involving inbreeding, of animals which have demonstrated their breeding worth through their progeny.

Family and Selection.—The term *family* is used to cover a wide degree of relationship. In taxonomic classification it occurs in the series phylum, class, order, family, genus, species. Such family members need be very slightly related and only so in relation to very distant common ancestors. The opposite of this is found in poultry where a family often means a set of full sibs. In animal breeding the term *family* can mean remote descendants of well-known sires or cows and having but slight relation-

ship. Or again it may mean a fairly closely related group of animals linebred to a certain animal. Finally, the term *family* can mean the two- or three-generation series of offspring and descendants from a foundation female, cow family, sow family, etc.

Up to now selection has been practiced preponderantly on an individual basis. In order to make selection more effective, its base now badly needs to be widened. This means that family selection, in the last-named sense, needs to be added to individual selection. In doing this, we must necessarily compromise to some extent. Whether to select an excellent individual from a relatively poor family or a relatively poorer individual from an excellent family poses many problems. Ideally, of course, we would select excellent individuals from excellent female families.

If we go back two generations on the bottom line of a pedigree, other offspring of this female (maternal granddam) are aunts and uncles of the animal being considered and their offspring are cousins. Other off-spring of the first-generation female (dam) are full or half brothers and sisters, and their offspring are nieces and nephews. The whole group makes up the female family, and the average merit of the group should be considered in selection, with relative weight being assessed according to degree of closeness of relationship; half cousins, $\frac{1}{2}^4$; full cousins, uncles and aunts, nieces and nephews, $\frac{1}{2}^3$; half brothers and sisters, $\frac{1}{2}^2$; and full brothers and sisters, $\frac{1}{2}$.

The breeder's main problem is that of recognizing favorable variations among his animals and assigning them to their proper source and cause, so that he may lay plans to capture, perpetuate, and increase them. This is an intricate problem at best, and in small herds or flocks it must be accomplished with rather inefficient tools. There are many pitfalls along the way.

In small herds or flocks using one male at a time, the offspring for a year or two will all be by this sire. There will be differences in these offspring which are likely to be attributed to their dams or female families. Since the males in use are far from homozygous, many of these differences should probably be attributed to them, but which ones or how much of those observed, it is impossible to say.

The variation between families is made up of the additively genetic, the environmental, and genetic sorts which are similar among members of the same family but different between families and the random environmental. In large families, where the members are closely related, the environmental and nonadditive genetic variations are small between families and the genetic similarities among family members exceed their phenotypic similarities, family selection can be most effective.

tion of 0.614 to the least accurate judge of −0.098. The average ability of these men is 0.246, or they are, on the average, about 25 percent better judges of dairy cattle for milk production than the average trained dairymen. Clearly, some men are good cattle judges. Equally clearly, some men cannot judge cattle for milk production by the use of the score card. Such being the case, the individual man will do well before he selects cattle by their conformation alone to make a sufficient test to convince himself that he is one of those gifted men who can judge dairy cattle.

On the other hand, almost anyone can weigh milk. No personal equation need be present in recording the weights. Such being the case, when they are obtainable the dairyman or buyer would do well to consider the milk yield carefully in selecting dairy cows as indicated by the figures above.

Table 36 shows the production by classified groups for several breeds of dairy cattle on a percentage basis calling "Excellent" 100 per cent.

It is evident from Table 36 that the higher scoring cows in all the dairy breeds are the more productive ones. However, there are enough good-type, low-producing cows and poor-type, high-producing cows in all the breeds so that the actual mathematical correlation between type and production is usually rather low—of the order of about 0.2. This means that selecting for good type would not necessarily give us high production and selecting for high production would not necessarily give us good type. If we want both, we must select for both and that means we must do some compromising, taking less of one in order to get more of the other.

TABLE 36.—BUTTERFAT PRODUCTION AVERAGES OF CLASSIFIED DAIRY ANIMALS IN TERMS OF PERCENTAGES

Classification groups	Ayrshire	Brown Swiss	Guernsey	Holstein	Jersey	Average of all
Excellent	100.0	100.0	100.0	100.0	100.0	100.0
Very good	91.8	89.6	92.4	92.2	95.2	92.2
Good plus	87.1	81.3	86.3	90.5	92.7	87.5
Good	83.2	75.7	84.4	85.4	89.8	83.7
Fair	80.2	.....	82.5	81.1	86.9	82.6

Correlation studies between type and production in classes of livestock other than dairy cattle have not been numerous. As would be expected, a fairly high correlation has been shown between weight and draft power in horses. In meat animals, type presumably is production, though many factors are concerned in the question as to whether the best type of animal will net the feeder the greatest profit, among the most important of which are the initial cost, the rate of gain, and the

efficiency of feed conversion. That there are considerable differences among animals in their ability to convert feed into flesh is well known, but there seems to be no evidence that this is associated with any specific type of characteristics.

The show ring has undoubtedly had a major place in shaping the type of all the classes of livestock. The first American show was held at Pittsfield, Mass., in 1810, and since that time many thousands of animals have passed before the judges' eyes. As now constituted, our livestock shows have both advantages and disadvantages from the standpoint of breed improvement.

Among the disadvantages are the following: (1) a possible lack of high correlation between showyard winning and efficiency of lifetime production; (2) a lack of opportunity to measure the transmitting abilities of the winning animals, except in a very limited manner through the "get of sire" and "produce of dam" classes; (3) the fact that "fitting" for the show ring often demands so great a departure from their "natural" condition by laying on great stores of fat (which often results in temporary or permanent sterility), removing a goodly portion of the wool in blocking, etc.; (4) the practice of remedying defects by surgical means; (5) the keeping of animals from productive work or from reproduction in order to enhance their likelihood of winning in the show ring; (6) the fact that clever fitting and showmanship can cover up weaknesses of various sorts; (7) the fact that commercialized show herds making a circuit of shows tends to discourage or prevent smaller local breeders from showing; (8) the fact that the offspring of top show winners are apt to be sought as sires more or less regardless of their own or their winning parents' actual genetic merit.

Yet in spite of these limitations, the show ring is the best medium yet discovered for molding breed type. This is probably its greatest advantage, but it has others, among them: (1) It brings breeders together for exchange of ideas and experiences; (2) it serves as the best advertising medium for both the breed and the individual breeder; (3) in a limited way at least it helps in discovering and popularizing the better genetic materials in the various breeds.

The show ring would be of greater service as an adjunct to breeding and selection (1) if it did not demand overfitting; (2) if the judges in all cases gave orally their reasons for their placings; (3) if in the classes of meat animals the animals could be slaughtered for carcass and cutout values; (4) if in horses a pulling and behavior test could be invoked, although it is realized that we want a steady all-day tractive exertion of 150 lb. rather than one of 1,500 lb. for 1 or 2 minutes; (5) if more weight could be given to the older breeding animals' actual accomplishments

as breeding animals; (6) if in dairy cattle a satisfactory combination based on both type and production could be utilized.[1]

In general, the livestock producer is interested in the type of animal that will make him the most money. Whether this is the type that is currently winning top honors at our livestock shows needs investigation. Since the show does wield such a great influence on type in the breeder's mind and since the breeder is interested primarily in profitable lifetime production, these two angles need constant scrutinizing and for the best interests of all concerned should be brought and kept in line.

Sometimes men waste time and effort in selecting for some mark that is supposed to be positively correlated with productivity. The best example of this was perhaps the old escutcheon theory, through which some men thought they could foretell the milk yield of dairy cattle by means of the hair pattern found on the rear and inside of the thighs. It has never been possible to prove the slightest connection between these two things, which in the light of common sense is not surprising. Some men think that a slight hump in the middle of a cow's back, a notch at the tail setting, or a heavy shoulder, etc., are correlated with high production. Selection based on all such things as these is missing the mark by a very wide margin.

Fertility and Health in Selection.—Earlier chapters of this book were devoted to fertility and sterility. Since, with most classes of livestock, usefulness and profitableness depend so largely on the number as well as quality of offspring produced, this is a matter that should receive a breeder's close attention in selection. In the purchase of mature breeding animals, one should ascertain their actual breeding history. If this is questionable or deficient, one would in general be much better off not to buy. In the purchase of mature males, semen tests will reveal the likelihood of fertility, though they cannot guarantee it in any special instance.

In the purchase of young animals with no breeding history, one must rely on the performance in this regard of its close ancestors and collateral relatives. Rate of fertility is, in the final analysis, controlled by the genes working through the endocrine glands and the genitalia and, of course, is greatly influenced by environmental conditions. No one cares for twin foals, few for twin calves. In sheep a certain proportion of twins is desirable, and in swine we want moderately good-sized litters. One should select, therefore, in a naturally fertile strain but avoid extremes. The size of the immediate litter in which a boar may have been born is of some consequence, but the fertility of the strain or family

[1] Such a proposal has been formulated by W. W. Swett and R. R. Graves of the Bureau of Dairy Industry and is published as *U.S. Dept. Agr. Misc. Pub.* 409.

is of great importance. Males in the other classes of livestock should be selected from fertile families and from dams that were regular breeders throughout their lifetime.

Much work has been done in plants in breeding up disease-resistant strains. In animals, there is little comparable to this as yet, but there is evidence that some strains of animals are more resistant to certain diseases and other troubles than are others, and in some instances at least this appears to have a definite genetic basis. Card and Roberts have reported experimental evidence that seems to prove that "resistance and susceptibility to infection by *Salmonella pullorum* (in poultry) are due, at least in part, to the existence of dominant hereditary factors." Lambert, Speelman, and Osborn[1] have reported considerable differences in resistance to encephalomyelitis among the different breeds of horses at the U.S. Range Livestock Experiment Station as Miles City, Mont.

In nature, disease susceptibility tends to be self-limiting, for the weak strains are not apt to leave so numerous a progeny as are the more resistant strains. In man this weeding out of the unfit and their bad genes is interfered with through hospitalization and the marvelous accomplishments of the medical profession. We are making beginnings along this line in our animals by means of vaccines and other preventives. Whether or not this is a wiser scheme than breeding and selecting animals with a natural immunity because of their genetic make-up, the future must determine. Some diseases have no doubt been conquered by genetic means; others, like bovine tuberculosis, we have practically conquered by destroying animals that reacted to the test; others, like hog cholera, we have learned to live with through the help of vaccines. Human and animal diseases must be controlled or conquered if man is to persist on this planet, and perhaps there is no one best method for use in all cases. Since it is difficult if not impossible to make money from diseased animals, the intelligent breeder should use all the means at his disposal for securing naturally fertile, healthy, vigorous, and resistant animals and avoid at any cost the introduction of disease itself or susceptibility to any disease into his herd or flock.

In this category also, we might call attention to certain known lethals in livestock, such as "bulldog" calves, cleft palate in pigs, skeletal defects

[1] Lambert, W. V., Speelman, S. R., and Osborn, E. B., Differences in Incidence of Encephalomyelitis in Horses, *Jour. Hered.*, **30**(8):349–352, 1939.

See also Webster, L. T., Heredity in Infectious Disease, *Jour. Hered.*, **30**(9):365–370, 1939, Gowen, J. W., Contributions of Genetics to Understanding of Animal Disease, *Jour. Hered.*, **28**(7):233–240, 1937; Murphy, J. M., *et al.*, Comparison of the Incidence of Udder Infection and Mastitis in Two Cow Families, *Cornell Vet.*, Vol. 34, No. 3, July, 1944.

in lambs, and closed colon in foals. These abnormalities are due to specific genes. In selection, some attention should be paid to them, and every effort made to avoid their introduction into a herd or flock.

Although in no sense a disease, such characteristics as red calves in Holsteins or Angus, bay color in Percherons, too light a red in Durocs, black skin spots in Chester Whites, etc., are from the purebred standpoint undesirable and should be guarded against by means of records and pedigrees as much as possible, although such things are often fairly successfully covered up. The same may be said for any character that detracts from an animal's quality as a member of a certain breed. Although many of these things are inconsequential from a utilitarian standpoint, they are of consequence from the standpoint of the pure breed. Only fertile, healthy, vigorous animals that are typical of their breed in all respects should be admitted to one's own group of purebreds.

Averages and Selection.—Since the environment may play such an important role in the actual productivity of any animal, it is important that the breeder give the matter some attention in making his selection of breeding animals. In dairy cattle, for instance, age, length of time pregnant, season of freshening, number of times milked, general health through the lactation period, etc., may have very important bearings on the actual amount of milk a cow produces in any given lactation. In order to compensate for these environmental influences, correction factors have been devised. The only two that are widely used are those for age at freshening and number of days or number of times milked. From the standpoint of genetics or breeding, the only differences with which the breeder is concerned are those having a genetic basis. He must attempt, therefore, to smooth out the environmental differences by correction factors or otherwise in order to make the performance of his animals comparable. Similarly, the growth rates of beef calves, the number of pigs that a sow bears and raises, the amount and quality of wool produced by sheep may be greatly influenced by the environment.

One of the best and easiest ways of compensating for these environmental influences is through the use of production averages. A cow might make 500 lb. of fat one year, 600 another, and 400 another. It is likely that her level of inheritance for butterfat production is nearer to the 500-lb. level than to the 600- or 400-lb. level. In all qualities that are variable and that may be expressed on more than one occasion, an average of several measurements will prove safer and more accurate than any one measuring. With several opportunities to express a certain quality, the high and the low expressions are likely to cancel each other, though they will not necessarily do this. For safety's sake, therefore, the average of many records of production or measurement should always

be applied to breeding animals in order, in so far as possible, to eliminate the influence of extremely good or bad environmental conditions. Along with the records that every breeder should keep must go the ability to judge and evaluate fairly a host of environmental conditions which play upon the lives and producing capacities of his animals. Only with this technique or art well developed will the breeder be able to arrive at the point where he can evaluate actual genetic differences on which, of course, the entire success of his effort as a livestock breeder depends.

Balance and Selection.—We have already discussed a number of general items that should be borne in mind in selecting breeding animals, although we have by no means exhausted the list. Additional items will be presented in the three following chapters as they apply specifically to certain classes of farm mammals. One further matter of a general nature should be mentioned at this point, *viz.*, that of always keeping in mind a general balance sheet between all the items which it may be the purpose of the breeder to attempt to incorporate into the genetic pool of his own herd or flock. It is generally very easy to be a radical, to go to extremes, and very difficult to stick to the middle of the road or to find the happy medium.

For example, in selecting the breeding animals, it would be easy to go to extremes in draft horses and attain great weight and power at the expense of movability; or, in fast horses, to attain great speed at the expense of such a high-strung, nervous organization as to make performance either in racing or reproducing difficult of attainment; in dairy cattle, to attain tremendous producing powers at the expense of regularity of reproduction over a long lifetime; in meat animals, to attain great ability to fatten at the expense of reproduction or, conversely, to attain great reproductive powers (twins in cattle, triplets or quadruplets in sheep, litters of 20 or 25 young in hogs) at the expense of vigor and general ability to yield a desirable carcass in a short period of time.

The good judge of livestock is a man who is able to balance successfully the defects of one animal against those of another. Likewise, the good livestock breeder is the one whose selection yields him a proper balance in his animals of all the various and sundry qualities they must possess if they are going to be profitable.

We all realize that it would be very much more simple to select for only one quality at a time and, when we had that thoroughly incorporated into our herd or flock, to start on the next item. The drawback to such a scheme is the fact that, while we are getting the one desirable quality we want established in our herd or flock, we may also be getting one or several very undesirable things established also, provided we are practicing no selection against them. For example, we might select for

nothing but high milk production in dairy cattle, and we could undoubtedly secure it, but if it came at the expense of badly pendulous and broken-away udders or lack of general vigor, disease resistance, or longevity, it might not be worth the price. Or we might practice selection for a 4 per cent butterfat test in Holsteins to the exclusion of all else. Again we could undoubtedly be successful in this aim, but, if we got it at the expense of a greatly lowered total amount of milk, it probably would not be worth this price.

From a practical standpoint, therefore, we must reconcile ourselves to the task of generally selecting for several things and also selecting against several things at the same time and trying in general to strike a happy medium, a balance, between the best and the worst in several respects.

The items that hinder selection most are different in the two sexes. In the male, it is the inability to test out enough young males so as to be sure of getting one of the better ones. Probably not more than 10 to 20 per cent of the male offspring of sires are ever used in breeding, and only an infinitesimal portion of these are properly tested before being put into heavy service. Most breeders pick males on the basis of type and pedigree and hope. Probably many of the best males in any class of animals are never used for breeding.

The main impediment to selection in females is the rapid turnover among these animals. If a cow is in a herd for 4 years (until she is 6 years old), she will drop 2 heifer calves and we must keep one of them to replace her—we do not have much choice. The choice may be a little wider in ewes and sows, but not much so. If we could have our choice among 10 or 15 females to replace each one that goes out, we could expect to have more rapid improvement, provided our criteria for selection were sound. With our present rapid turnover among females little range of selection is possible. Anything a breeder can do to lower the rate of turnover in his herd will be of immediate benefit economically and of ultimately great benefit genetically.

Summary.—We have seen in this chapter that intelligent selection of breeding animals presents a great variety of problems. The main purpose of selection is to increase our stock of desirable genes and to diminish our stock of undesirable ones. Since we cannot examine the genes themselves, our only recourse is to estimate them by studying individuality, pedigree, and progeny. In addition to the difficulty of not being able to read the labels on the genes directly, there are the further complications due to dominance, epistasis, and probably other unknown interactions between the genes, as well as those caused by the environment. To be effective, our selection must be on the basis of variation caused by

genes, since environmental variations so far as is known are in no sense hereditary.

The breeder must first study his probable market and produce what the market is anxious to buy. He must then select the breed of animals that will best fulfill his own peculiar market demands. His individual selections must be guided by individuality, pedigree, and progeny performance. He must select for the type of animal that will most efficiently serve the production needs of his market over a long life of usefulness, a type set, it is to be hoped, by the show ring. He must above all else select fertile, healthy, vigorous individuals from strains or families of similar qualities, and he must base his selection on high average lifetime production rather than on the basis of single, exceptional performances. Selection, the key to animal breeding, is a many-sided problem. To weigh properly all the factors involved is far from easy, but on the success of such weighings a breeder's ultimate success depends as on no other one consideration.

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[1] See also the various breed histories.

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CHAPTER XXI

SELECTION IN DAIRY CATTLE

We have now finished our delineation of the principles underlying the improvement of animals. In this and the two following chapters we must get down to practical cases and indicate how the principles can actually be applied. We will cover many phases of practical selection, though we cannot, of course, cover all of them in all of their possible permutations and combinations. Each choice of males or females, each mating, each herd, each breed presents special problems. Only the person on the spot at the moment can supply the best answer, make the most nearly correct selection, and then only if he understands the basic principles involved and has good judgment and a reasonable amount of experience. We will start these practical chapters with a consideration of selection in dairy cattle.

Dairy cattle are found on about 75 to 80 per cent of the farms in the United States, and their products account for about 15 per cent of the total farm income. Of the 25 million dairy cattle in the United States, only about 5 per cent are purebred and registered, the remainder being 80 per cent grades and 15 per cent nondescripts. The average production of all dairy cattle is estimated to be about 5,000 lb. of milk a year. Dairying is thus seen to be one of the most important phases of animal husbandry and one greatly in need of improvement as far as the machinery of production, the individual cow, is concerned. Dairying is of special importance near the large centers of population.

In one respect, selection of dairy cattle is somewhat easier than with other classes of farm mammals, for a measure of a cow's producing ability in terms of milk and butterfat may be secured over her whole productive life. We can thus have tangible evidence of her average yearly lactation yield as well as that of her female offspring, though such actual records are available on only 4 to 5 per cent of our dairy animals. In another respect, dairy-cattle selection is more difficult than in other livestock classes, since it is difficult, if not impossible, to estimate from the exterior form what the internal functioning will yield in terms of milk and butterfat. In this class of livestock, too, the male cannot evidence the quality for which the species is kept; *i.e.*, the bull yields no milk, so that his genetic quality can only be measured through the performance of his offspring, male and female. Selection is further complicated in dairy

cattle by the fact that breeders desire their animals to evidence the approved dairy type in addition to being high and profitable producers, and the two things are not highly correlated.

Genetically, we are faced with the very serious problem that milk production is the end result of a long chain of events caused by manifold and complex physiological functionings, which probably means that many genes and many kinds of gene interactions are involved. What we are trying to do, therefore, is to ascertain the genetic causes of very complicated physiological processes in a species which has many chromosomes and few offspring. With 30 pairs of chromosomes, 2^{30} gametic recombinations of paternal and maternal chromosomes are possible and 3^{30} possible zygotes (to say nothing of dominance and epistatic effects, crossing over, mutations, and chromosomal aberrations), and at best we can have only a few score or hundreds of daughters of a bull and three or four or five daughters of a cow. We may get a few landmarks, but the details of the genetic picture are quite likely to be blurred and the whole seeming picture turn out to be a mirage.

Another obstacle militating against the effectiveness of selection in dairy cattle is the fact that neither type nor production are completely heritable. For example, Lush, Norton, and Arnold (1941), in a study of the effects which selection of dams may have on sire indexes, report heritability figures of 28 per cent for fat and 33 per cent for milk based on Iowa D.H.I.A. records and from Holstein H.I.R. data figures of 25 per cent for fat when based on the first lactation and 30 per cent when based on the second lactation. Lush and Straus (1942) found a value of 17 per cent for heritability of butterfat production in dairy cattle. They also cite Ward's figure of about 25 per cent as revealed by his study of New Zealand cattle. And likewise, in dairy-cattle type, Tyler and Hyatt (1948) report a figure of about 30 per cent for heritability of type ratings between parent and offspring in dairy cattle.

The fact that type and production are not completely heritable does not mean that we should not select from best-type and highest producing cows. We must of course do this. What the relatively low heritability figures mean is that individual looks and performance must be augmented by as many other favorable indications as can be secured from performance of an animal's close relatives and the performance of its offspring.

In addition to all the above handicaps, the environment can play mean tricks on us and lead us astray. Milk production is a highly elastic affair, easily influenced by men, money, materials; feeding, fussing, fertilizing; health and general hocus-pocus, as well as heredity. Finally, the cow is forced to live, produce, and reproduce under conditions very far removed from what might be called natural ones.

In spite of the difficulties, enormous progress has been made in improving both the type and the productiveness of our dairy animals. We have no pictures of the general type of cow that our savage, cave-dwelling, or nomadic ancestors tended, but it seems certain that it would win nothing but derision or a laugh if exhibited in a modern show ring. The earliest cows produced enough milk to help nourish their calves for 1, 2, or 3 months, a few hundred pounds at the outside, whereas many thousands of D.H.I.A. cows average over 8,000 lb. of milk yearly, and the record production by a single cow stands close to 42,000 lb. of milk in a year. Progress has been made, and breeders have made it for the most part with the presently considered clumsy tool of a belief in the old adage that "like begets like," or phenotypic selection. Most breeders still find this tool useful, but it can be sharpened considerably by considering records of performance on the part of collateral relatives, as well as ancestors and progeny.

A hunt for superior germ plasm in dairy cattle was instituted by the Bureau of Dairy Industry in 1936. In all, a total of 1,097 herds of dairy cattle were surveyed that had continuous records for a long enough period to have proved at least two sires on the basis of comparing their daughters' and their mates' records. Of these, 708 herds located in 40 states and including seven breeds had complete enough data to be included in the summary, of which 157 herds were deemed to have made progress, the other 551 not. The 17 foundation cows, which was the average number, in the 157 herds averaged 447 lb. of fat; the 62 average additions to these herds averaged 498 lb., giving a cumulative average of 487 lb. of butterfat. The remaining 551 herds had an average of 15 foundation cows with records averaging 433 lb. of fat; the 40 additions averaged 431 lb. of fat with a cumulative average of 431 lb. A total of 4,309 sires were used in the 708 herds, and 2,242 of them could be proved through five or more daughter-dam comparisons. About 32 per cent of these bulls raised production of their daughters over their dams; 20 per cent held it; and 48 per cent lowered it. The average herd reported on six sires, which left a total of 39 daughters whose production was 451 lb. of butterfat, while their dams had averaged 452 lb. A few herds had made fairly steady progress, a few had steadily gone downhill in production, most had had ups and downs. A few samples of this are shown in Table 37.

When it is recalled that the above figures are for the better dairy herds, one can well imagine what the total story on all dairy herds in the United States would be. In general, it would appear that we have been breeding average cows to average bulls, and we can, of course, expect to get average offspring. Better means of discriminating between our own

TABLE 37.—CASE HISTORIES OF BREEDING FROM BUREAU OF DAIRY INDUSTRY IN TERMS OF YEARLY BUTTERFAT AVERAGES

	Herd A	Herd B	Herd C	Herd D
Foundation cows	318	372	327	435
Daughters of 1st sire	369	366	377	373
Daughters of 2d sire	408	363	421	336
Daughters of 3d sire	495	374	346	291

female lines, and sharper tools for use in the selection of males are badly needed.

The most important item in the dairy business is the individual cow. If she is healthy, a good producer, long-lived, and able to transmit her good qualities to numerous offspring, then there is a firm foundation for the multitude of activities that must result before milk, butter, cheese, or ice cream appear on the consumer's table. If, on the other hand, the individual cow is not healthy, not a good producer, not long-lived, and worse still, probably capable of transmitting these poor qualities to her offspring, then the whole of the dairy industry rests on a very insecure foundation. It is clear, therefore, that dairymen cannot devote too much time and thought to the matter of getting better cows into their dairy herds.

Selection Goals in Dairy Cattle.—Breeders of dairy cattle want their herds to exhibit many qualities of which the following is a partial list: production, test, efficiency, persistency, longevity, disease resistance, regularity of breeding, good disposition, easy milking, good type, trueness to breed standards, etc. It should be obvious that, with so many things clamoring for attention, considerable compromising is bound to ensue. It would not be so bad if we had easily applied objective measurements for all these wanted things, but for many of them, all we can have is a subjective judgment, an opinion which may be right or may be wrong and may be variable. Many things in our above list can be measured objectively, but only over a period of years, yet we must select from some of our cows while they are young. Our above list could perhaps be grouped under two headings: (1) physical individuality or type, (2) physiological individuality, which adds up to production and reproduction.

Dairy Type and Selection.—Dairy type has been more or less of a moot subject for a long time. In fat stock type is production to a considerable extent. In hogs, for example, a long deep body (loin and rib chops and bacon), well-fleshed front and rear ends (shoulder, butt, and ham), with smoothness, quality, and nonwastefulness indicates directly to the eye that the five primal cuts make up a considerable portion of the

live animal. In dairy cattle the degree of correlation between type and production is not nearly so high. Nevertheless, type does enter into the selection picture for dairy cattle, and, when successful, it pays very good dividends possibly as regards reproduction, probably as regards production, certainly as regards sales merit. Type is an old means of evaluating animals, having appeared in Roman animal husbandry writings of nearly 2,000 years ago. In those far-off days the bovine was used primarily as a draught animal, and the ideal animal was to be well made; sound, deep-bodied; with long, thick neck; broad, high shoulders; a wide, deep body; good rump; short, straight legs; good hoofs; and a smooth, soft hide. Included with these points. which obviously have some bearing on power, were stipulations that the animal have dark horns, hairy ears, flat nose, black muzzle, tail reaching to the heels, and preferably be black in color—points which might be described as fancy rather than strictly utilitarian. With this for a starter, or even without it, it is not surprising that dairy-cattle score cards continue to carry aesthetic as well as utilitarian requirements.

The presently used score card for dairy cows of all breeds allots 30 points to general appearance, 40 points to dairy character and body capacity, and 30 points to mammary system. It seems impossible to quarrel with the latter two divisions which have to do with size and quality of body and udder. Many statistics are available which show that the larger cows within a breed are, generally, more productive and profitable than are the smaller ones. Quality is more difficult to measure, but experience has shown that, generally, cows of a lean, angular type, of moderate-sized bone, of thin hide, and with udders which, when milked out, are soft and yielding, thus indicating no overdevelopment of connective tissue, are higher milkers than those with the contrasting attributes. But, whether one pays any attention to so-called "type" in practicing selection, or not, he is probably going to select cows which are *lean* in the neck, shoulder, and thigh; *deep* and *wide* in body and flank; and carrying a *capacious mammary system of high quality*. So, we repeat, that these 70 points on the present score card are fully justified and are probably used by all progressive dairy-cattle breeders.

The only possible score-card argument then boils down to the matter of the 30 points for general appearance. These 30 points demand that the animal conform, within certain limits, to the generally accepted breed standards and that its head and lean neck, its capacious body, and its large, quality udder, show some decent relationship to each other, and that the body be carried on fairly straight and well-placed legs which (following Abraham Lincoln's stipulation) are at least long enough to reach to the ground.

It appears, then, that the critics of "type" make much ado about nothing. True, how pretty a cow's face is (and judgments would differ as they seem to do in our own species), how straight her back, how level her rump, how pretty her legs, probably have little to do with how productive she is. But, both "dirt farmer" and "real breeder" know

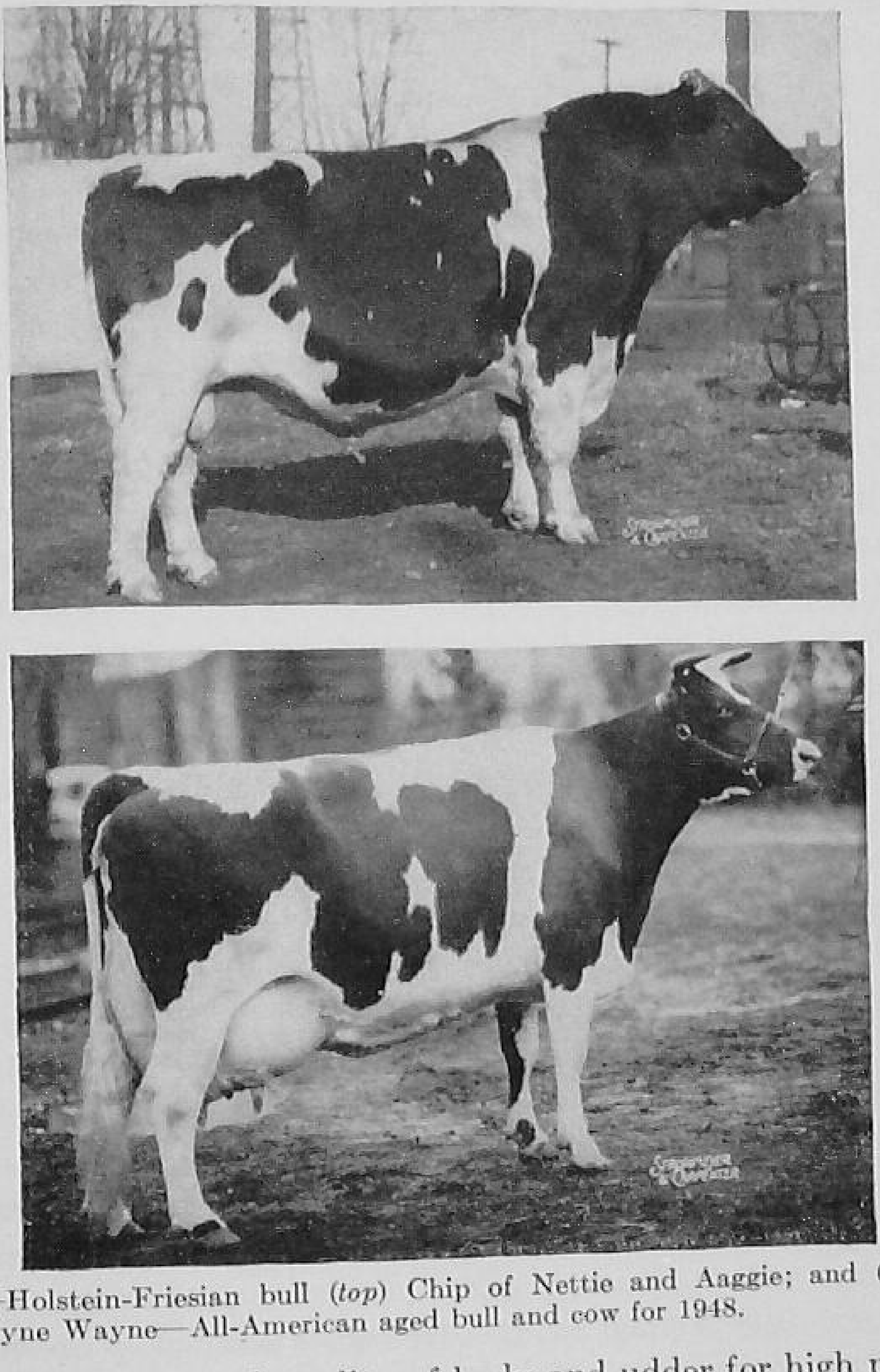


FIG. 170.—Holstein-Friesian bull (*top*) Chip of Nettie and Aaggie; and (*bottom*) cow, Rosehill Fayne Wayne—All-American aged bull and cow for 1948.

they must have size and quality of body and udder for high production, and with the udder strongly attached—not sagging to within a few inches of the ground and being kicked like a football at every step. The bodily essentials for milk production we all agree on—some "practical" men will take them no matter how poorly they are joined together, just as long as they are still in one piece—the "breeder" wants the same things, but wants them blended together into a symmetrical whole. Now it

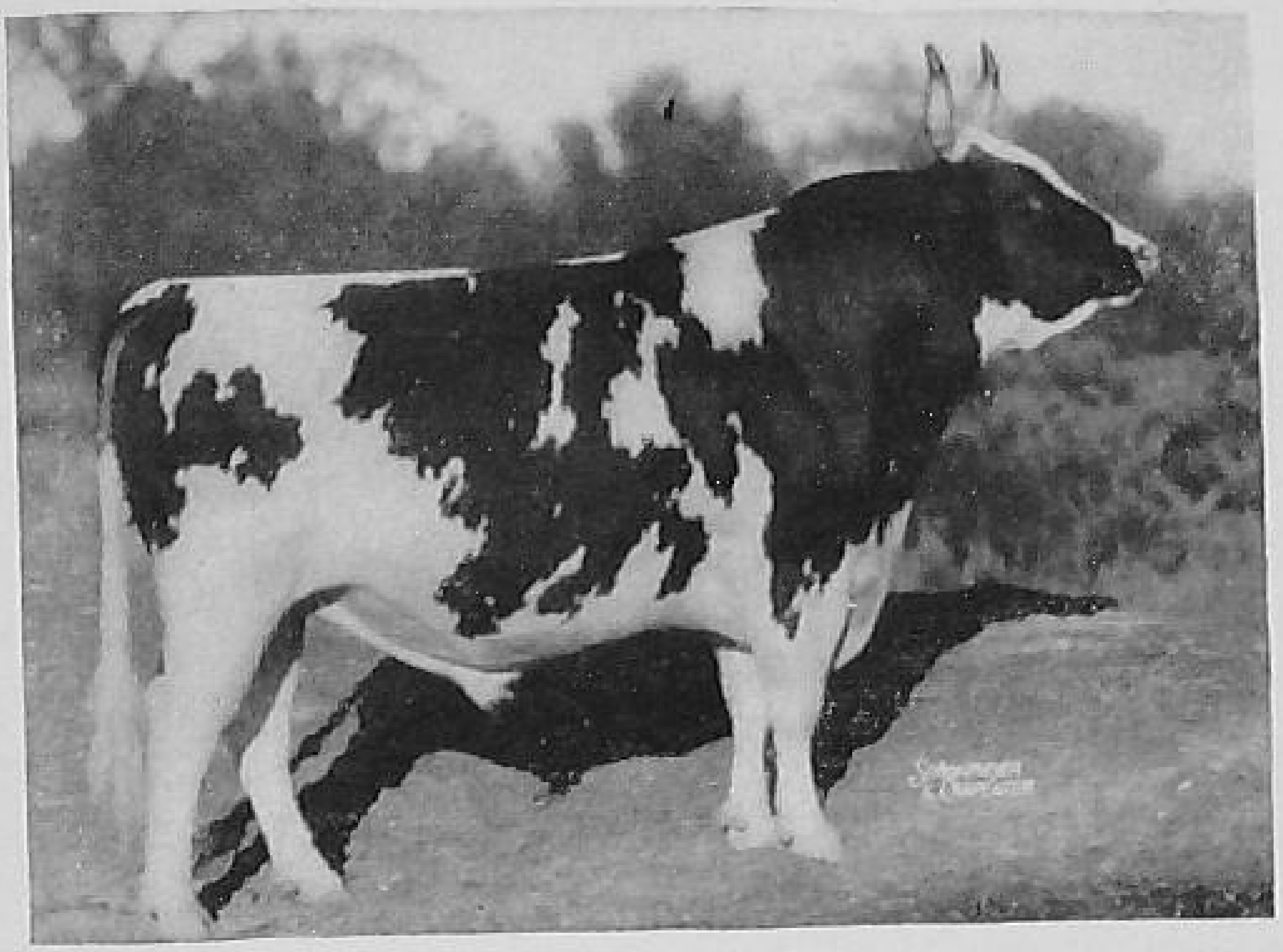
should be obvious that the man who tries to get the necessities more properly blended has a more difficult task, but he gets good dividends for his efforts when successful, both in satisfaction and sales appeal as well as to some extent in production and perhaps in longevity.

Some people apparently have the erroneous idea that "dairy type" was conceived in one or a few minds sometime in the dim past, and that selection for this type gradually led to increased production. The exact opposite is probably the truth—selection for production gradually brought "dairy type" into being; *i.e.*, cows which put excess feed into milk rather than into fat on their backs are just naturally lean and angular. It is certain, therefore, that the individuality (type) of a dairy cow is *an indication* of whether the animal will be a good producer or not. Type is not an infallible guide to production, but it is, within limits, a sound guide. Since "like tends to beget like" (again not perfectly), we can get some idea of how an animal will transmit from its own type, and we should continue to use individuality in trying to measure the probable transmitting abilities of our breeding females. Most breeders do select heifers (and bulls) from their best-type and highest producing cows. Type and production of daughters of these "best" cows do not always equal or exceed the dams—the correlation between type or production of dams and daughters is not perfect—but what we get from this procedure is certainly well worth having.

There are two biological reasons why there is not a perfect correlation between type and production of daughters and dams. The first reason is that inheritance is a halving and sampling process. Each animal is likely to get some good and some poor hereditary determiners from each parent. In some eggs (or sperm) the sample half may contain most of the good hereditary units and a few of the poor ones, or most of the poor ones and a few of the good ones. Many varying sample halves are possible. So, our "best" cows do not always transmit fully their own excellencies, and can and do transmit differently to their various offspring—the very nature of the hereditary process makes it almost certain that this will be so. The other biological reason for the low correlation between dams and daughters is the fact that each daughter must have another parent (a bull), and he, too, transmits samples of his inheritance—some better, some worse. In addition to these two biological reasons for lack of complete type and production correlation between dams and daughters, there are also the environmental differences in feeding and management, which may lead to rather extreme differences between dams and their daughters.

There is a decided relation, as numerous statistics show, between size and producing capacity in dairy cattle. Other things being equal, the

big cow produces more and returns more over feed cost than does the little cow in any breed or in grade animals. Again, this is not to say that all big cows are good producers and all small cows poor producers. Our experience contradicts such a statement, but it is true that we will more often find high production in big dairy cows than we will in small



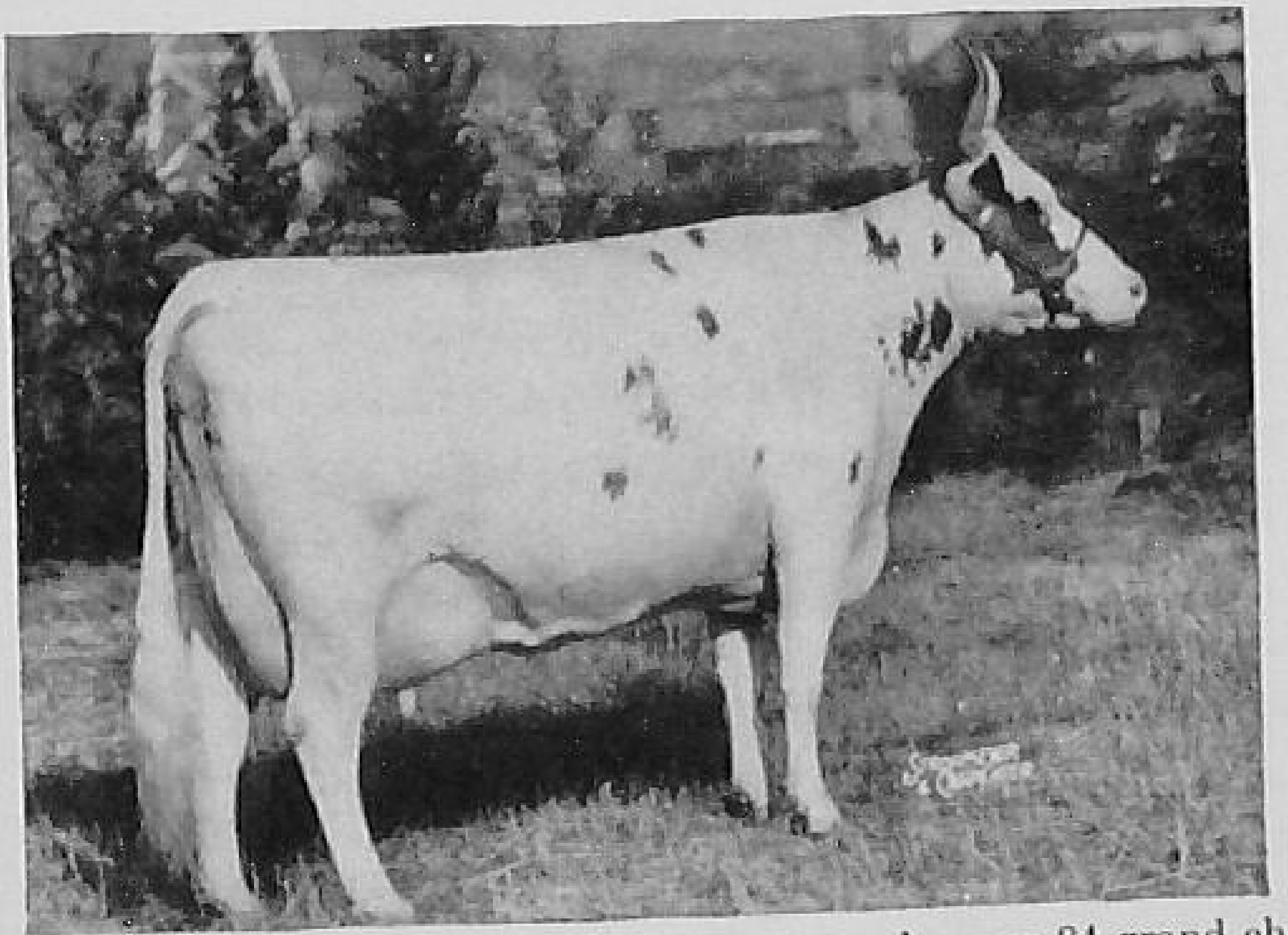


FIG. 171.—Ayrshire bull (*top*) Netherhall Swanky Dan who won 84 grand championships; and cow (*bottom*) Alfalfa Farm Ann 2nd, a many times grand champion cow.

ones. Therefore, good size for the breed or grade is a point to be kept in mind in the selection of replacements.

Included in size is the matter of length, depth, and width of body. The animals should be deep from the top of the withers to the floor of the chest, should be comparatively wide through the chest region, should be deeper through the rear than through the foreflank. The ribs should

leave the backbone at as much of a right angle as possible and be wide between. Such conformation gives ample room for the vital organs, heart, and lungs, and generally indicates the proper bodily mechanism for the consumption and digestion of large quantities of feed.

Another important consideration as to type is that of dairy quality. By this is meant the form of the external characteristics, which evidence the probable ability and willingness of the animal to consume and digest large amounts of feed beyond her maintenance requirements and the ability also to convert this feed into milk rather than into flesh or fat. These characteristics are evident to the practiced eye, much as they may have been derided by those who like to scoff at type. Among them are a clean-cut face; prominent, bright eye; wide, strong muzzle; long lean neck; thinness and fineness over the withers; spread between the ribs; length, width, and leanness through the rump; leanness through the thighs; fineness of hair and of bone; and thinness and mellowness of hide. These characteristics generally accompany the high milk producer and can be accepted as marks indicative of good dairy production, not as we have stated above, in an infallible sense, but by and large they will hold true.

The third item, in addition to size and dairy quality, is that of udder quality and capacity. The udder is the working portion of the dairy cow. It should be large. It should be attached well up between the hind legs and well forward on the underline. It should not be broken away and pendulous, and it should have a level sole. The udder should be of good quality; *i.e.*, when milked out, it should be soft and yielding, indicating the presence of enough, but no excess, connective tissue, which does not, of course, aid milk secretion. The udder of a high-producing cow is generally well supplied with veins that are evident to the eye. The udder should show as little cleft between the right and left halves as possible, and no cleft between the front and rear quarters as viewed from the side. There should be four teats of uniform size placed toward the four corners of the udder, though not, ideally, exactly at the corners.

The blood, carrying food materials to the udder, flows from front to rear along the upper portion of the cow and then descends down through the udder and flows back to the heart, through veins known as the *milk veins*. These veins pass forward from the udder on the underline and should disappear through the body wall somewhere near the front legs. These veins should be large and generally tortuous. If large and tortuous, this can generally be taken as indicating a good flow of blood through the udder. The general type of the dairy cow should indicate strength together with quality. The animals should be of good size but show no coarseness. The practiced eye of the dairyman catches the

indication of femininity and quality in a dairy cow. There should be evidence of strength throughout, as indicated by a relatively straight topline, width and depth of chest, straightness and strength of legs when viewed either from the side or the rear. The dairy cow is a hard-working animal, and, if she is to perform her work over a long period of time, she must be of a rugged, strong constitution. At the same time, she must show femininity, quality, and animation.

Good-type animals are more likely to have good-type offspring than are poor-type animals. For this reason, and even though the correlation is considerably less than 1.0, it will pay to select from our better type individuals. Figure 172 shows the type distribution of 5,616 daughters of classified cows in one of our dairy breeds.

Dams \ Daughters	Ex.	V.G.	G+	G	F	P
Ex.	22	85	95	86	6	
V.G.	48	351	516	448	76	2
G+	29	281	710	673	127	6
G	25	209	488	817	167	18
F	4	20	92	154	44	5
P		2	2	5	3	

FIG. 172.—Distribution of classified daughters from classified dams.

Excellent cows do not beget only excellent daughters; poor cows do not beget only poor daughters. However, we are more likely to get good-type offspring from the three upper classification types than from the lower three. The correlation is not high (about 0.2) but it is positive. From a study of 3,738 paternal sisters and of 1,601 cows out of classified dams, Tyler and Hyatt arrived at the conclusion that the heritability of type was about 30 per cent; *i.e.*, that offspring inherit about one-third the superiority or inferiority of the parents' type. If we had the average-type score of both the male and female parents, the correlation would probably be higher.

Most of our dairy-breed associations now provide for type classifications for their breeders. Some of the breeds print the types of the animal classified. Such information is valuable, but it leaves a lot to be desired. When the record shows a certain cow to be G+, we do not know whether she was off in general appearance, body capacity, dairy quality, or mammary system, or how much in each. When all a bull's daughters

average G+ in udders, we do not know whether they were scored down for small udders, unbalanced udders, poorly attached udders, poor teat placement, or something else.

The danger with type classification is twofold: (1) We are inclined to assume we are getting more information than is actually the case. If we want to know what kind of daughters a certain bull had, no amount of data on any printed page will substitute equally for a trip to inspect the daughters at first hand, and to round out the picture, we should study their dams as well. (2) The other danger comes from using the data superficially. Some breeders take the stand that they will not use any bull whose dam has not classified as excellent. We have nothing against the dam of a bull classifying "Excellent"; but if, as often happens, the inference is that the bull's daughters will be of superior type (because his dam was "Excellent"), we must hasten to object. The only proper way to use classification data as a selection tool is by comparing the average of all of a bull's daughters with the average of the dams of those daughters. If a bull was bred to cows which averaged 80 per cent in type and his daughters averaged 85 per cent, you know that the bull was a good transmitter of type; but even so you should strive to know a lot more about the details than this general, over-all type of score average gives you.

Still another drawback to type is that animals do look differently on different days and in various stages of lactation. We find that we get a truer judgment of a cow's genotype for production from an average of several records than from any one by itself. The same thing would probably hold for type.

A recent study by Hyatt, Tyler, and Conklin (1949) with 102 Ayrshires classified several times (6, 12, 18, 24+ months) showed that 5 per cent classified the same as cows as they had as heifers, 51 per cent varied 1 grade, 38 per cent varied 2 grades, and 6 per cent varied 3 grades. Part of this variation was due to type changes in animals, especially probably in feet and legs and udders; part was due to the fact that there were nine official classifiers who worked on the project with no doubt some differences among judges and in the same judge on different days.[1]

The correlation between the average of the several ratings of each heifer before first calving and the first and second ratings after calving were 0.37 and 0.40 respectively. With improvements in and standardization of classification methods, particularly for heifers, the classification program may become valuable

[1] Hyatt, G., Jr., Tyler, W. J., and Conklin, C. T., The Relationship between Type Ratings of Ayrshire Females as Young Heifers and as Cows, *Jour. Dairy Sci.*, 32(4).380, 1949.

in helping breeders to cull the poorest type individuals from their herds at an early age.

Since dairy type has sales value (more for some breeders than for others), is partially correlated with production and perhaps with longevity, and is up to one-third heritable, it should receive attention from dairy-cattle breeders in their selection plans and on a family as well as individual basis. An animal which herself scores 95 per cent, but whose parents, grandparents, uncles, aunts, cousins, half brothers and sisters, and nieces and nephews average 80 per cent is not likely to be as good a transmitter of type as one which herself scores 85 per cent and whose close relatives also average 85 per cent. The breeder will be recompensed for selecting from good-type animals, especially if the latter are members of good-type families.

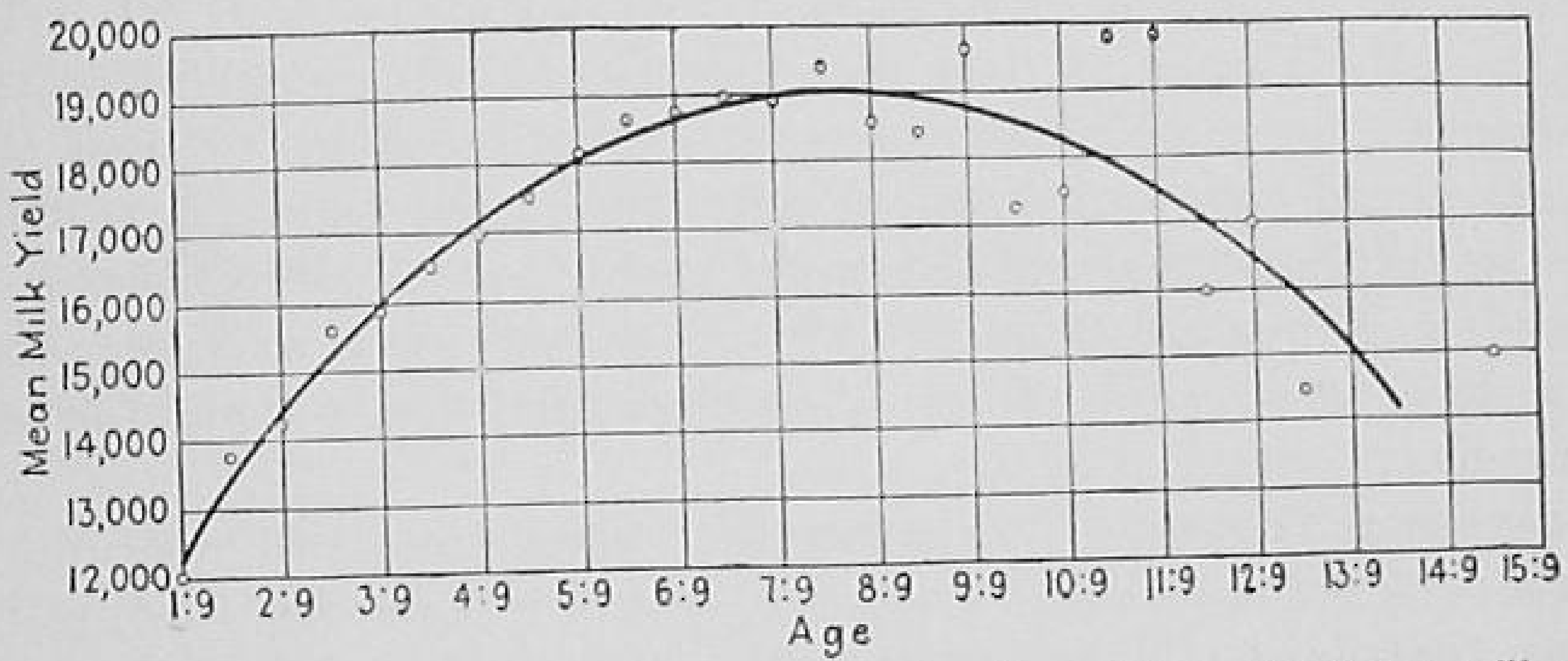


FIG. 173.—Observational and fitted curves showing the relation of 365-day milk yield to age for Holstein-Friesian cattle. The observational curve is represented by small circles. The smooth curve shows the fitted logarithmic curve for milk yield. (*From Gowen, Studies in Milk Secretion, Me. Agr. Expt. Sta. Report,* 1920.)

Should a breeder pay attention to type in his selection of bulls? The answer is yes—perhaps unfortunately so. If he keeps poor-type bulls and uses their pictures in illustrated advertising, his farm will be avoided as a source of breeding stock.

There is little correlation between the type of a bull and the type of his get—there is no known correlation between the type of a bull and the production of his get. If a bull himself is of good type and his direct ancestors and collateral relatives are also and he is mated to "typy" cows from "typy" families, he probably will sire good-type offspring, and they do sell for more than those of poor type.

Selecting for excessively good type in dairy bulls has probably retarded increased production to a considerable degree. It should be enough to have our bulls average or better in type. Too much attention to type makes us compromise on production. We do not favor selection for production alone and paying no attention to type, nor do we favor

selecting for type alone and paying no attention to production. A reasonable balance must be sought and it will not be easily found.

Production and Selection.—Since dairy cattle are maintained primarily for the purpose of converting roughages, grain, and grain by-products into milk and butterfat, it is not surprising that production bulks large in most selection schemes for dairy cattle. Like good type, high records have advertising and sales value; they are 16 to 30 or 40 per cent heritable; and since many studies have shown that the return over feed cost moves steadily upward with increasing production, the matter of basing selection mainly on production would seem to be justified. The manner in which animal breeding still gropes in the dark because of a lack of factual data on individual accomplishments may be visualized through the fact that in the class where it is easiest to get objective records, namely, dairy cattle, only about 4 per cent of cows enrolled are in D.H.I.A. which together with cows on AR test make the tested total probably less than 5 per cent. For more rapid progress in animal breeding, we need more factual data on which to base our judgment in selection. It seems to come awfully hard, and what we get is likely to serve advertising needs more than it does genetic ones. Before the individual milk records of cows can be most useful, they must be placed on some comparable basis by means of conversion factors.

Conversion Factors.—It is a fact that most cows will continue to produce more milk and butterfat yearly from the time they first freshen as two-year-olds up to the age of six to eight years, and that thereafter the amount of butterfat and milk will gradually decline in amount. For this reason age-conversion factors for amount of milk have been devised, generally from the average production of many thousands of cows at the various ages. Butterfat test generally drops slightly with advancing age (increasing production), but the change is so slight that we generally do not attempt to apply conversion factors to butterfat per cent.

The age-conversion factors for amount of milk are probably in reality growth or weight-conversion factors. The decline in the size of the factors from two to six to seven years of age corresponds to an increase in size toward full maturity, the rise in the size of the factors from six to seven years of age on is probably due to some general slowing down with advancing age plus the likelihood of udder injuries. What we want is a measure of the cow's productive ability at her prime—necessarily compensated for in youth or old age.

Various sets of age- and times-milked conversion factors are given in the accompanying tables. These tables show what cows do "on an average" as they increase in age or in times milked. They are suitable, therefore, for converting groups of daughters' and dams' records to a

TABLE 38.—GENERAL CONVERSION FACTORS

To convert a 365-day record to a 305-day basis multiply by	0.85
To convert a 305-day record to a 365-day basis multiply by	1.17
To convert a 4-times-a-day milking to 3-times-a-day milking multiply by	0.88
To convert a 4-times-a-day milking to 2-times-a-day milking multiply by	0.74
To convert a 3-times-a-day milking to 4-times-a-day milking multiply by	1.13
To convert a 3-times-a-day milking to 2-times-a-day milking multiply by	0.83
To convert a 2-times-a-day milking to 3-times-a-day milking multiply by	1.20
To convert a 2-times-a-day milking to 4-times-a-day milking multiply by	1.35
To convert 2 milkings per day for 305 days to 3 milkings per day for 365 days add	40 %
To convert 3 milkings per day for 365 days to 2 milkings per day for 305 days subtract	30 %

TABLE 39.—AGE-CONVERSION FACTORS, D.H.I.A. DATA, U.S.D.A.

Age	Ayrshire, Guernsey, Jersey	Brown Swiss, Milking Shorthorn	Holstein	Mixed average of Ayrshire, Guernsey, Jersey, and Holstein
1–6	1.343	1.718	1.515	1.429
2–0	1.262	1.538	1.377	1.319
2–6	1.195	1.400	1.275	1.235
3–0	1.141	1.286	1.203	1.172
3–6	1.099	1.196	1.131	1.115
4–0	1.063	1.136	1.077	1.070
4–6	1.037	1.088	1.035	1.036
5–0	1.020	1.052	1.017	1.018
5–6	1.008	1.028	1.006	1.007
6–0	1.000	1.012	1.000	1.000
6–6	1.000	1.006	1.000	1.000
7–0	1.000	1.000	1.006	1.003
7–6	1.006	1.000	1.012	1.009
8–0	1.012	1.000	1.018	1.015
8–6	1.018	1.000	1.036	1.027
9–0	1.024	1.006	1.054	1.039
9–6	1.035	1.012	1.072	1.053
10–0	1.047	1.030	1.090	1.068
10–6	1.064	1.048	1.114	1.089
11–0	1.082	1.072	1.138	1.110
11–6	1.100	1.096	1.162	1.131
12–0	1.112	1.114	1.192	1.152
12–6	1.124	1.132	1.222	1.173
13–0	1.136	1.144	1.252	1.194
13–6	1.148	1.156	1.282	1.215
14–0	1.160	1.168	1.306	1.233
14–6	1.172	1.174	1.330	1.251
15–0	1.184	1.180	1.348	1.266
15–6	1.193	1.186	1.366	1.279
16–0	1.199	1.192	1.378	1.288

TABLE 40.—FACTORS FOR REDUCING PRODUCTION RECORDS TO A TWICE-A-DAY MILKING BASIS

Number of days milked	3 times daily	4 times daily
5–15	0.9903	0.9831
6–25	0.9839	0.9721
26–35	0.9776	0.9614
36–45	0.9713	0.9509
46–55	0.9652	0.9406
56–65	0.9591	0.9306
66–75	0.9531	0.9208
76–85	0.9472	0.9111
86–95	0.9414	0.9017
96–105	0.9356	0.8925
106–115	0.9299	0.8834
116–125	0.9242	0.8746
126–135	0.9187	0.8659
136–145	0.9132	0.8573
146–155	0.9077	0.8490
156–165	0.9024	0.8408
166–175	0.8971	0.8328
176–185	0.8918	0.8249
186–195	0.8866	0.8171
196–205	0.8815	0.8096
206–215	0.8764	0.8021
216–225	0.8714	0.7948
226–235	0.8665	0.7876
236–245	0.8616	0.7806
246–255	0.8567	0.7736
256–265	0.8520	0.7668
266–275	0.8472	0.7601
276–285	0.8425	0.7536
286–295	0.8379	0.7471
296–305	0.8333	0.7407

standard basis as is necessary in indexing sires—they will not necessarily work in individual cases.

The writer has proposed the set of factors shown in Table 41 for converting Guernsey AR records to a standard 3×, 365, mature basis.

Some AR records are for numbers of milkings other than 610, 730, 915, or 1,095. Conversion factors to take care of this are shown in Table

TABLE 41.—AGE AND CLASS CONVERSION FACTORS FOR GUERNSEY AR RECORDS

Age	365 day 3× 1,095 M	305 day 3× 915 M	365 day 2× 730 M	305 day 2× 610 M
Jr. 2	1.26	1.47*	1.51†	1.76‡
Sr. 2	1.21	1.42	1.45	1.69
Jr. 3	1.16	1.36	1.39	1.62
Sr. 3	1.11	1.30	1.33	1.55
Jr. 4	1.08	1.26	1.30	1.51
Sr. 4	1.04	1.22	1.25	1.46
Jr. 5	1.02	1.19	1.22	1.43
Sr. 5	1.01	1.18	1.21	1.41
Jr. 6	1.00	1.17	1.20	1.40
Sr. 6	1.00	1.17	1.20	1.40
Jr. 7	1.00	1.17	1.20	1.40
Sr. 7	1.00	1.17	1.20	1.40
Jr. 8	1.01	1.18	1.21	1.41
Sr. 8	1.02	1.19	1.22	1.43
Jr. 9	1.03	1.20	1.23	1.44
Sr. 9	1.04	1.22	1.25	1.46
Jr. 10	1.05	1.23	1.26	1.47
Sr. 10	1.06	1.24	1.27	1.48
Jr. 11	1.07	1.25	1.28	1.50
Sr. 11	1.08	1.26	1.30	1.51
Jr. 12	1.09	1.27	1.31	1.53
Sr. 12	1.10	1.29	1.32	1.54
Jr. 13	1.11	1.30	1.33	1.55
Sr. 13	1.13	1.32	1.36	1.58
Jr. 14	1.14	1.33	1.37	1.60
Sr. 14	1.15	1.34	1.38	1.61
Jr. 15	1.16	1.36	1.39	1.62

* Column 2 times 1.17.
† Column 2 times 1.20.
‡ Column 2 times 1.40.

42, and it would be unnecessary to have these conversion factors if all records were reported as either of 305 or 365 days duration.

Finally in Tables 45 and 46 are to be found factors which will put records of any sort onto a 305, 2×, mature basis.

What we are interested in is a cow's ability to convert feed into food efficiently and over a long lifetime. Since the fat per cent between breeds varies and also the fat per cent among cows in the same breed, Gaines and Davidson have suggested a method for converting milk of any test to a given standard per cent of Fat Corrected Milk. The standard most generally used is that of 4 per cent F.C.M. (Fat Corrected Milk). The factors for this are 0.4 times total milk + 15 times total butterfat.

TABLE 42.—FACTORS FOR INCREASING PARTIAL 3× RECORDS TO ENTIRE 3×,305 AND 3×,365

305-day records		365-day records	
No. of milkings	factor	No. of milkings	factor
610–615	1.200	730–735	1.200
616–625	1.188	736–745	1.190
626–635	1.181	746–755	1.184
636–645	1.173	756–765	1.177
646–655	1.165	766–775	1.171
656–665	1.158	776–685	1.165
666–675	1.151	786–795	1.159
676–685	1.144	796–805	1.153
686–695	1.137	806–815	1.147
696–705	1.130	816–825	1.141
706–715	1.123	826–835	1.135
716–725	1.116	836–845	1.129
726–735	1.109	846–855	1.123
736–745	1.102	856–865	1.117
746–755	1.096	866–875	1.112
756–765	1.089	876–885	1.106
766–775	1.083	886–895	1.100
776–785	1.076	896–905	1.095
786–795	1.070	906–915	1.089
796–805	1.064	916–925	1.084
806–815	1.058	926–935	1.079
816–825	1.052	936–945	1.073
826–835	1.046	946–955	1.068
836–845	1.040	956–965	1.063
846–855	1.034	966–975	1.058
856–865	1.028	976–985	1.053
866–875	1.022	986–995	1.048
976–885	1.017	996–1,005	1.043
886–895	1.011	1,006–1,015	1.038
896–905	1.005	1,016–1,025	1.033
906–915	1.000	1,026–1,035	1.028
		1,036–1,045	1.023
		1,046–1,055	1.018
		1,056–1,065	1.014
		1,066–1,075	1.009
		1,076–1,085	1.005
		1,086–1,095	1.000

TABLE 43.—AYRSHIRE AGE-CONVERSION FACTORS

1-3, 1-4, 1-5	1.412						
1-6, 1-7, 1-8	1.377						
1-9, 1-10, 1-11	1.338						
2- 0	1.294	7- 0	1.000	11- 0	1.070	15- 0	1.167
2- 1	1.279	7- 1	1.001	11- 1	1.072	15- 1	1.170
2- 2	1.264	7- 2	1.002	11- 2	1.074	15- 2	1.173
2- 3	1.250	7- 3	1.003	11- 3	1.076	15- 3	1.176
2- 4	1.236	7- 4	1.004	11- 4	1.078	15- 4	1.179
2- 5	1.222	7- 5	1.005	11- 5	1.080	15- 5	1.182
2- 6	1.211	7- 6	1.006	11- 6	1.082	15- 6	1.185
2- 7	1.199	7- 7	1.007	11- 7	1.084	15- 7	1.188
2- 8	1.188	7- 8	1.008	11- 8	1.086	15- 8	1.191
2- 9	1.176	7- 9	1.009	11- 9	1.088	15- 9	1.194
2-10	1.167	7-10	1.010	11-10	1.090	15-10	1.197
2-11	1.159	7-11	1.011	11-11	1.092	15-11	1.200
3- 0	1.149	8- 0	1.012	12- 0	1.094	16- 0	1.203
3- 1	1.142	8- 1	1.013	12- 1	1.096		
3- 2	1.135	8- 2	1.014	12- 2	1.098		
3- 3	1.127	8- 3	1.015	12- 3	1.100		
3- 4	1.119	8- 4	1.016	12- 4	1.102		
3- 5	1.111	8- 5	1.017	12- 5	1.104		
3- 6	1.103	8- 6	1.018	12- 6	1.106		
3- 7	1.095	8- 7	1.019	12- 7	1.108		
3- 8	1.089	8- 8	1.020	12- 8	1.100		
3- 9	1.082	8- 9	1.021	12- 9	1.112		
3-10	1.076	8-10	1.022	12-10	1.114		
3-11	1.071	8-11	1.023	12-11	1.116		
4- 0	1.064	9- 0	1.024	13- 0	1.118		
4- 1	1.059	9- 1	1.025	13- 1	1.120		
4- 2	1.054	9- 2	1.026	13- 2	1.122		
4- 3	1.049	9- 3	1.028	13- 3	1.124		
4- 4	1.045	9- 4	1.030	13- 4	1.126		
4- 5	1.041	9- 5	1.032	13- 5	1.128		
4- 6	1.036	9- 6	1.034	13- 6	1.130		
4- 7	1.033	9- 7	1.036	13- 7	1.132		
4- 8	1.031	9- 8	1.038	13- 8	1.134		
4- 9	1.028	9- 9	1.040	13- 9	1.136		
4-10	1.026	9-10	1.042	13-10	1.138		
4-11	1.024	9-11	1.044	13-11	1.140		
5- 0	1.020	10- 0	1.046	14- 0	1.142		
5- 1	1.018	10- 1	1.048	14- 1	1.144		
5- 2	1.016	10- 2	1.050	14- 2	1.146		
5- 3	1.013	10- 3	1.052	14- 3	1.148		
5- 4	1.011	10- 4	1.054	14- 5	1.150		
5- 5	1.009	10- 5	1.056	14- 5	1.152		
5- 6	1.007	10- 6	1.058	14- 6	1.154		
5- 7	1.006	10- 7	1.060	14- 7	1.156		
5- 8	1.005	10- 8	1.062	14- 8	1.158		
5- 9	1.004	10- 9	1.064	14- 9	1.160		
5-10	1.003	10-10	1.066	14-10	1.162		
5-11	1.002	10-11	1.068	14-11	1.164		
6- 0	1.000						

TABLE 44.—FACTORS FOR COMPUTING INCOMPLETE RECORDS TO A 305-DAY BASIS By 5-day Periods. Ayrshire Data

Days	Factor	Days	Factor	Days	Factor	Days	Factor
1–7	38.76	80	2.81	155	1.61	230	1.19
10	29.18	85	2.66	160	1.56	235	1.17
15	16.58	90	2.53	165	1.53	240	1.16
20	11.99	95	2.41	170	1.49	245	1.14
25	8.00	100	2.31	175	1.46	250	1.13
30	6.98	105	2.22	180	1.43	255	1.12
35	5.98	110	2.12	185	1.40	260	1.10
40	5.31	115	2.04	190	1.37	265	1.09
45	4.74	120	1.98	195	1.35	270	1.07
50	4.29	125	1.91	200	1.32	275	1.06
55	3.93	130	1.85	205	1.29	280	1.04
60	3.62	135	1.80	210	1.27	285	1.04
65	3.37	140	1.75	215	1.25	290	1.03
70	3.16	145	1.70	220	1.23	295	1.02
75	2.96	150	1.65	225	1.21	300	1.01

It would be impossible to determine superiority between a cow which made 20,000 lb. of 3 per cent milk and 600 lb. of butterfat and one which made 14,000 lb. of 5 per cent milk and 700 lb. of butterfat. Applying the above factors, however, gives us (20,000 × 0.4) 8,000 + (600 × 15) 9,000 = 17,000 lb. of 4 per cent F.C.M. for the first animal and (14,000 × 0.4) 5,600 + (700 × 15) 10,500 = 16,100 lb. of 4 per cent F.C.M. for the second. The first cow transformed more feed energy into milk energy than did the second without regard to the efficiency of the transformation. The figure 17,000 lb. of 4 per cent F.C.M. for the first cow means that in making 20,000 lb. of 3 per cent milk she transformed as much feed energy into milk energy as she would have done if she had made 17,000 lb. of 4 per cent milk.

The breeder in any breed will have cows which vary quite a bit in butterfat test. A method is available for converting milk of any test to any standard. The procedure is based on the figures for converting to 4 per cent F.C.M., namely, 0.4 of the milk plus 15 times the total butterfat. One pound of 5.3 per cent milk is equal to 1 × 0.4 = 0.4 plus 0.053 × 15 = 0.795 or 1.195 lb. F.C.M. and the figures for converting milk of any test to a standard 5.3 per cent F.C.M. are obtained by dividing (0.4 M. + 15 F.) by 1.195, which gives us milk times 0.3347 and total fat times 12.55.

These factors for the various breeds are found in Table 47. With the breed factors in Table 47, a breeder can put the production of all his cows into the standard F.C.M. for his breed and thus smooth out

TABLE 45.—HOLSTEIN CONVERSION FACTORS

Age	2×,305	2×,365	3×,305	3×,365	4×,305	4×,365
1–6	1.515	1.287	1.257	1.06	1.121	0.953
2–0	1.377	1.170	1.143	0.964	1.019	0.866
2–6	1.275	1.084	1.058	0.892	0.944	0.802
3	1.203	1.022	0.998	0.842	0.89	0.757
3–6	1.131	0.961	0.939	0.792	0.837	0.711
4	1.077	0.915	0.894	0.754	0.797	0.677
4–6	1.035	1.880	0.859	0.724	0.766	0.651
5	1.017	0.864	0.844	0.712	0.753	0.640
5–6	1.006	0.855	0.835	0.704	0.744	0.633
6	1.000	0.85	0.83	0.7	0.74	0.629
6–6	1.000	0.85	0.83	0.7	0.74	0.629
7	1.006	0.855	0.835	0.704	0.744	0.633
7–6	1.012	0.860	0.840	0.708	0.749	0.637
8	1.018	0.865	0.845	0.713	0.753	0.640
8–6	1.036	0.880	0.860	0.725	0.767	0.652
9	1.054	0.896	0.875	0.738	0.780	0.663
9–6	1.072	0.911	0.890	0.750	0.793	0.674
10	1.090	0.926	0.905	0.763	0.807	0.686
10–6	1.114	0.947	0.925	0.780	0.824	0.701
11	1.138	0.967	0.945	0.797	0.842	0.716
11–6	1.162	1.988	0.964	0.813	0.860	0.731
12	1.192	1.013	0.989	0.834	0.882	0.750
12–6	1.222	1.039	1.014	0.855	0.904	0.769
13	1.252	1.064	1.039	0.876	0.926	0.787
13–6	1.282	1.090	1.064	0.897	0.949	0.806
14	1.306	1.110	1.084	0.914	0.966	0.821
14–6	1.330	1.130	1.104	0.931	0.984	0.836
15	1.348	1.146	1.119	0.944	0.998	0.848

DAYS MILKED*

305–308	1.00	337–340	0.92
309–312	0.99	341–344	0.91
313–316	0.98	345–348	0.90
317–320	0.97	349–352	0.89
321–324	0.96	353–356	0.88
325–328	0.95	357–360	0.87
329–332	0.94	361–364	0.86
333–336	0.93	365	0.85

* Applicable also to Table 46, hence omitted there.

differences in butterfat test. The most usual figures which breeds print about their cows are those for total milk and total fat. These figures are the least valuable to the breeder. What he needs to know are his animals' fat test (because it does not generally pay to stray too far from breed average in this respect) and total inheritance for production. He

TABLE 46.—GUERNSEY AND JERSEY CONVERSION FACTORS

Age	2×,305	2×,365	3×,305	3×,365
1–6	1.343	1.142	1.115	0.940
2	1.262	1.073	1.047	0.883
2–6	1.195	1.016	0.992	0.836
3	1.141	0.970	0.947	0.799
3–6	1.099	0.934	0.912	0.769
4	1.063	0.904	0.882	0.744
4–6	1.037	0.881	0.861	0.726
5	1.020	0.867	0.847	0.714
5–6	1.008	0.857	0.837	0.706
6	1.000	0.850	0.830	0.700
6–6	1.000	0.850	0.830	0.700
7	1.000	0.850	0.830	0.700
7–6	1.006	0.855	0.835	0.704
8	1.012	0.860	0.840	0.708
8–6	1.018	0.865	0.845	0.713
9	1.024	0.870	0.850	0.717
9–6	1.035	0.880	0.859	0.725
10	1.047	0.890	0.869	0.733
10–6	1.064	0.904	0.883	0.745
11	1.082	0.920	0.898	0.757
11–6	1.100	0.935	0.913	0.770
12	1.112	0.945	0.923	0.778
12–6	1.124	0.955	0.933	0.787
13	1.136	0.966	0.943	0.795
13–6	1.148	0.976	0.953	0.804
14	1.160	0.986	0.963	0.812
14–6	1.172	0.996	0.973	0.820
15	1.184	1.006	0.983	0.829

TABLE 47.—CONVERSION FACTORS TO VARIOUS F.C.M. STANDARDS

	Av. test	Conversion factors	
		Milk	Total fat
Ayrshire	4.06	0.396	14.84
Brown Swiss	3.96	0.402	15.10
Guernsey	4.90	0.353	13.20
Holstein	3.55	0.429	16.09
Jersey	5.30	0.3347	12.55

should, therefore, know the fat test of each cow, and if he will convert all production to his own breed standard F.C.M. test by means of the factors in Table 47, he will have each cow's total production figure.

For more rapid progress in improving dairy cattle, we need more production facts, and these facts must be standardized to some common basis by means of age and times-milked factors, and the F.C.M. factors will add a further refinement of the data.

Methods for Indexing Dairy Bulls for Production.—Since a dairy bull yields no milk, his transmitting inheritance must be assayed by means of his type, his pedigree or the production facts of his offspring. The first two methods are not very accurate. Over the past 30 years, many suggestions have been made for working out the third method. In general, the idea is to try to get a genetic picture of the bull by studying his daughters' records or by comparing them with those of their dams.

Pearl, Gowen, and Miner[1] (1919) suggested the quartile method of arriving at a bull's transmitting ability. This method consists of plotting the curve of variability of AR records, dividing it into quartiles (or octiles), then classifying the offspring of each sire in terms of percentage on the basis of the relative standing of each dam with her daughter. The highest quarter of the AR records was called A, the second B, the third C, and the fourth D. If a bull had 4 daughters, and 50 per cent, or 2, of them were in the second quarter, whereas the respective dams were in the first quarter; 1 daughter, or 25 per cent, was in the second quarter, whereas her dam was in the third quarter; and 1 daughter, or 25 per cent, was in the fourth quarter, whereas her dam was in the first quarter; the bull was then represented by the following formula, the dams' letters being given first:

$$50AB + 25CB + 25AD$$

The example just given seems relatively simple, but on occasion this formula for a bull can become very complicated; *e.g.*, the formula for Spermfield Owl:

$$12AA + 4AB + 4AC + 23BA + 12BB + 4BC + 8CA + 8CB + 4CD + 12DA + 4DB + 8DD$$

In any event, the method was complicated and too indefinite for general use. In any given case the question for which a breeder seeks an answer is, How many pounds of milk and what fat percentage will this bull transmit to his daughters? No such definite answer is possible by the quartile method.

[1] Pearl, R., Gowen, J. W., and Miner, J. R., *Maine Agr. Col. Ext. Bul.* 281, (Studies in Milk Secretion VII), 1919.

Yapp[1] (1925) advanced the theory that a sire's potential transmitting ability might be expressed in terms of 4 per cent milk by the formula $X = 2A - B$. Here X = the sire's potential transmitting ability, A = the daughters' average records converted to a 4 per cent fat basis, and B = the dam's record converted to a 4 per cent fat basis. This is tantamount to saying that the average production of the daughters falls just halfway between the average production of the dam's and sire's potential transmitting ability. We have here the adoption of the theory, borne out quite generally in nature, that the crossing of the two extremes will produce progeny about halfway between the parents if the character is determined by multiple factors, as no doubt milk production is. It is comparatively simple, of course, to find the bull's index, provided the dams' and the daughters' average productions are known. This method is unfortunate in that it hides in one figure details that a breeder should know, *viz.*, the potential amount of milk and the percentage of fat which the bull transmits. The method of converting records to a 4 per cent basis as practiced by Yapp was based on the above-mentioned Gaines and Davidson[2] formula of 0.4 of the milk plus 15 times the fat equals the F.C.M. to a standard 4 per cent basis.

Table 48[3] gives the factors for standardizing milk of any test to a 4 per cent F.C.M. basis.

TABLE 48.—FACTORS FOR CONVERTING WEIGHTS OF MILK OF OTHER FAT CONTENT TO THEIR ENERGY-EQUIVALENT WEIGHT OF 4.0 PER CENT MILK

f*	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
2	0.700	0.715	0.730	0.745	0.760	0.775	0.790	0.805	0.820	0.835
3	0.850	0.865	0.880	0.895	0.910	0.925	0.940	0.955	0.970	0.985
4	1.000	1.015	1.030	1.045	1.060	1.075	1.090	1.105	1.120	1.135
5	1.150	1.165	1.180	1.195	1.210	1.225	1.240	1.255	1.270	1.285
6	1.300	1.315	1.330	1.345	1.360	1.375	1.390	1.405	1.420	1.435
7	1.450	1.465	1.480	1.495	1.510	1.525	1.540	1.555	1.570	1.585

* *f* = fat percentage.

Turner[4] (1925) proposed the following formula as a means of ascertaining a bull's index: Sire's potential transmitting ability equals the daugh-

[1] YAPP, W. W., Transmitting Ability of Dairy Sires, *Amer. Soc. Anim. Prod. Proc.* December, 1924.

[2] GAINES, W. L., and DAVIDSON, F. A., Relation between Percentage Fat Content and Yield of Milk, *Ill. Agr. Expt. Sta. Bul.* 245, 1923.

[3] PERKINS, A. E., A Simplified Procedure for Calculating Weights of Milk, etc., *Jour. Dairy Sci.*, **20**:129–132, 1937.

[4] TURNER, C. W., A Comparison of Guernsey Sires, *Mo. Agr. Expt. Sta. Res. Bul.* 79, 1925.

ter's fat production minus 0.15 of the dam's fat production divided by 0.85. This formula grew out of Turner's study in which he found that for each increase of 100 lb. of fat on the part of the dams, the daughters increased 15 lb. This formula of Turner's implies the genetic theory of partial dominance on the part of the bull, since the daughters are seen to progress 85 per cent of the way up or down to the bull's level from the dam's average level of production.

Graves[1] (1926) suggested comparing the dams' and daughters' records and letting the difference (plus or minus) stand for the bull's index. In rating bulls under this system, Graves also considered the average milk production of the dams and daughters, the average fat percentage of dams and daughters, and the percentage of daughters making an increase in amount of milk as well as the percentage making an increase in fat test.

Goodale[2] (1927) proposed the Mt. Hope bull index. This assumed that, in matings between animals of unequal levels, milk production is on the average about seven-tenths of the distance above the level of the lower parent, while butterfat per cent is about four-tenths of the distance above the lower level. To get the Mt. Hope Index, compute the average mature equivalent of the milk production of all daughters of the bull, also the average mature equivalent of the milk production of the dams of these daughters and take the difference between these averages.

If the daughters' average exceeds the dams' average, add three-sevenths (or 0.4286) of the difference to the daughters' average to get the bull's milk-index figure.

If the daughters' average is less than the dams' average, subtract seven-thirds (or 2.333) of the difference from the daughters' average to get the bull's milk-index figure.

The index for percentage of butterfat is obtained by similar operations, but with different fractions.

If the daughters' butterfat average percentage exceeds the dams' butterfat average percentage, add three-halves (or 1.5) of the difference to the daughters' average to get the bull's butterfat index.

If the daughters' average is less than the dams' average, subtract two-thirds (or 0.6667) of the difference from the daughters' average to get the bull's index.

The above was known as the Precise Mt. Hope Index. Later it was suggested to ignore the theoretical partial dominance of high milk yield and low fat test and consider that the daughters fell halfway between

[1] GRAVES, R. R., Transmitting Ability of 23 Holstein-Friesian Sires, *U.S. Dept. Agr. Bul.* 1372, 1926.

[2] GOODALE, H. D., Selecting a Herd Sire, Mt. Hope Farm Publication, 1927.

dams and sire index in both milk and test. This is a variation of the idea expressed by Yapp and others earlier.

Gifford[1] (1930) from a study of a group of Guernsey bulls concluded that the daughters' records could be used as the index of the bull. In other words, the dam's contribution is disregarded entirely, which is all right provided the dams in each instance are an average of the breed.

Wright[2] has proposed a method for evaluating bulls that takes into account the number of daughter-dam pairs available. He has clarified the situation by distinguishing between three types of matings. The first type, a mating of a bull with some individual cow, Wright says, can be answered by using the method of multiple regression, provided all the necessary correlation coefficients are available. Even this, however, would seem to be rather a risky procedure in the present state of probable heterozygosity of most of our dairy animals. The second type of matings of a bull to cows in the same herd or of similar levels of production, Wright says, can be foretold by the records of the previous daughters of the bull.

For the answer to the question as to what record would be expected of daughters of a bull, if the latter were mated with a random sample of cows of the breed, Wright has proposed the following formula:

$$S = \frac{2}{n+2} A + \frac{n}{n+2} (2O - D)$$

where n = the number of daughter-dam comparisons; A = the breed average in production; O = the daughters' average production; D = the dams' average production; and S = the bull's index. This system is based on the genetic theory of multiple-factor inheritance and gives added weight to the breed average, where the number of daughter-dam comparisons is small and increasing weight to the daughter-dam comparisons as the number of these increases.

At the present time, the dairy-bull index that is being most used is the one which places the daughters exactly halfway between the production level of their dams and the index of their sire, both for amount of milk and percentage of fat. This is now generally known as the Equal-parent Index. First, we must convert the milk records of cows to which a bull was mated to some standard basis by means of conversion factors given above; do the same thing to the daughters' records; and, when we have gotten all the records onto a comparable basis, make a comparison

[1] GIFFORD, W., The Mode of Inheritance of Yearly Butterfat Production, *Mo. Agr. Expt. Sta. Res. Bul.* 144, 1930.

[2] WRIGHT, S., On Evaluation of Dairy Sires, *Amer. Soc. of Anim. Prod. Proc.*, 1931, pp. 71–78.

between the average production of the dams and the average production of the daughters. The simplest way to do this is by the formula—twice the daughters' averages for milk and test minus those of the dams. This lets the daughters fall just halfway between the actual average production of the dams and the estimated index of the bull, on the assumption that both parents are jointly and equally responsible for the characteristics of their offspring.

Dams					Daughters				
Age of cow	Actual record	Conversion factor	Converted record	Test	Age of cow	Actual record	Conversion factor	Converted record	Test
2	7,841	× 1.262 =	9,895	4.91	3½	7,422	× 1.099 =	8,157	5.21
2	8,263	× 1.262 =	10,428	5.06	4	8,347	× 1.063 =	8,873	5.10
3½	9,340	× 1.099 =	10,265	4.83	2	7,250	× 1.262 =	9,149	5.00
6	11,521	× 1.000 =	11,521	5.21	3½	9,351	× 1.099 =	10,277	4.98
4	10,842	× 1.063 =	11,525	4.96	2½	10,461	× 1.195 =	12,500	5.03
6	9,560	× 1.000 =	9,560	5.01	3	7,340	× 1.141 =	8,375	5.12
			6/63,194	6/29.98				6/57,331	6/30.44
			10,532	4.99				9,555	5.09

All records—305-day lactations

Average of dams	10,532 − 4.99
Average of daughters	9,555 − 5.09
Difference	− 977 + 0.10
Bull's index	8,578 − 5.19

FIG. 174.—Bull-index work sheet. For a worth-while index the first 6 to 10 daughters of a bull must be tested and their average production compared with that of their dams. We could select 6 daughters of almost any bull and thereby give him a fairly high index, which might have a large advertising value, but its genetic value would be almost zero. Average production over a period of years gives a much truer estimate than does the production of any one year.

A bull index is a very useful tool in the selection and breeding of dairy animals, though it should by no means be the only one. Figure 174 shows the index of a given bull with the dams' records on the left and the daughters' records on the right, both sets converted to standard mature age, six years, 305 days lactation, twice-a-day milking. Since records show that the fat test of milk produced by a cow is relatively constant, *i.e.*, changes little, although it does fall slightly with age, it is not customary or necessary to apply any conversion factors to the butterfat test. The bull comes out with an index of 8,578 lb. of milk and a 5.19 per cent test on 6 daughter-dam pairs. It would have been better, of course, for the bull to have had 8 or 10 daughters rather than 6, and they must be

the first 6 or 10 daughters; *i.e.*, they cannot be a selected 6 or 10 and yield anywhere near accurate results.

Regression Index.—One of the authors[1] recently examined the bull-index problem and proposed a new index called Regression Index. The regression of groups of daughters' records on those of groups of dams was found to be 0.5.

The matter of regression may be easily illustrated by a graph, as in Fig. 175.

In Fig. 175, we have assumed a breed with an average production of 10,000 lb. If we graph the groups of cows from 6,000 to 14,000 lb. (solid line), then the average of their daughter groups will fall about on the broken line starting at 8,000 lb. and rising to 12,000 lb. From 6,000-lb. dams, we "normally expect" to get daughters at the 8,000-lb. level; *i.e.*, they will regress one-half of the way back up to the breed average. Likewise, from 14,000-lb. dams, we "normally expect" their daughters to regress one-half of the way back down to the breed average.

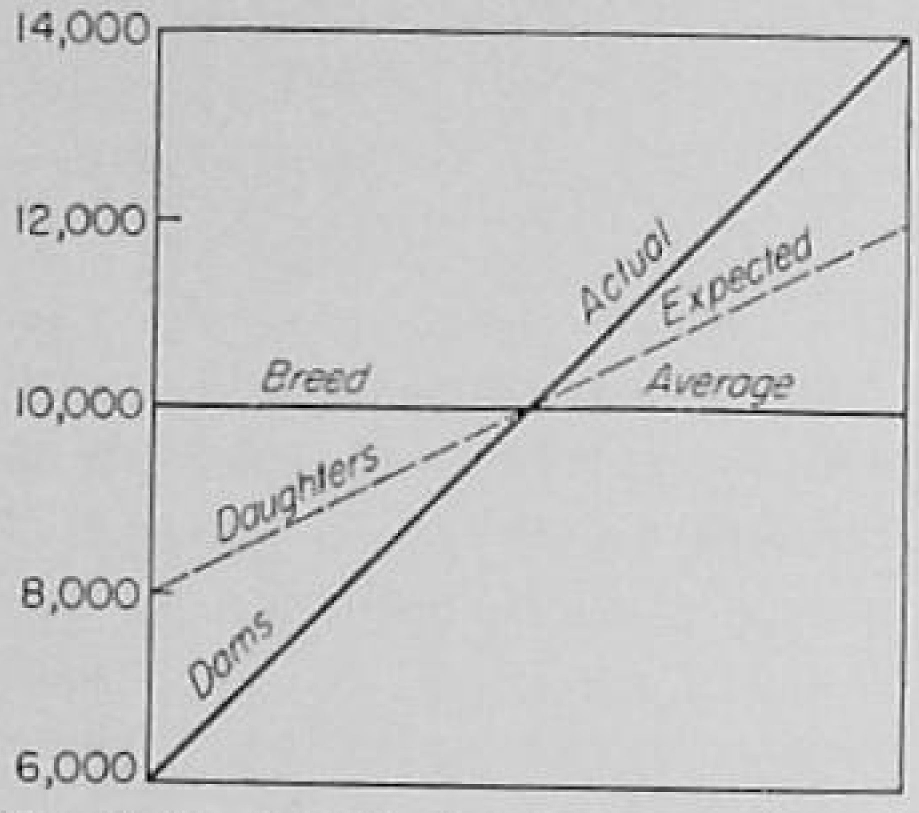


FIG. 175.—Graph showing regression of groups of daughters on groups of dams.

Regression, however, is not a mysterious natural law. It is due to two things: (1) the fact that phenotype does not necessarily truly mirror genotype (especially in a quality like milk production which is so prone to environmental influences), and (2) that animals producing toward the extremes are unlikely to be mated to animals as extreme as themselves.

If the breed average is 10,000 lb. of milk, we normally expect a group of daughters averaging 8,000 lb. from a group of cows averaging 6,000 lb. Whether we would get this or not from any particular bull would remain to be seen. From a dozen bulls we might get groups of daughters all the way from 10,000 or 12,000 lb. down to 6,000 lb., but the average of all of them would be about 8,000. There is no mysterious force, regression or any other, which will tend to move a 6,000-lb. herd up to 8,000 lb. If the owner continues to use bulls with a transmitting level of 6,000 lb., his herd will stay at the 6,000-lb. level, but if he uses average bulls, it will climb up toward 8,000 lb. Likewise, a 14,000-lb. herd will not automatically drop to 12,000 lb. This herd is likely to fall back toward the breed average because its owner is likely to use average bulls. If he

[1] RICE, V. A., A New Method for Indexing Dairy Bulls, *Jour. Dairy Sci.*, **27**(11): 921–936, 1944.

uses bulls with an inheritance of 14,000 lb. or more, his herd will remain at 14,000 lb.

Regression (first used by Francis Galton) is, in one sense, an unfortunate term because to most minds it usually connotes going backward. In the biological sense, it means, according to Webster, "the correlation between parent and offspring when used as a measure of inheritance." Actually, of course, regression is the correlation times the ratio of the two standard deviations, but since in much biological data the two standard deviations are approximately equal, the correlation and the regression often have approximately the same value in studies of heredity. Regression is commonly referred to as "the drag or boost of the breed." When animals get below the breed average, their offspring "tend to" climb back up toward the breed average; when they get above the breed average, they "tend to" fall back toward the breed average. In short, regression moves upward from below the breed average and downward from above the breed average.

The regression index can be found by getting the difference between his daughters' actual and "normally expected" production and adding this difference to the breed average. This proposal differs from the Equal-parent system in that the latter method deals with the actual records of dams and daughters without specific reference to the breed average, although, as will be shown, this feature could be included.

The Regression Index could be calculated from tables centered on the respective breed averages both for amount of milk and for butterfat test, with daughters' expectation rising or falling from the breed average one-half as fast as their dams.

If tables of normal expectation were not available, the normal expectation for any group of daughters could be ascertained by adding the respective breed averages in milk and test to the dams' average in milk and test and dividing by 2.

The easiest way of finding a bull's Regression Index would be to find his Equal-parent Index in the usual fashion (twice the daughters' averages minus the dams), then add the respective breed averages for milk and test to this Equal-parent Index and divide by two. In other words, the Regression method simply regresses the Equal-parent indexes halfway back to the respective breed averages.

Formulae for finding the Equal-parent and Regression indexes are as follows:

$$\text{Equal-parent} = W + 2(d - e)$$
$$\text{Regression} = W + (d - e)$$

where W = breed average, d = daughters' actual production (or test) and e = daughters' expected production (or test). Leaving the figure 2

out of the Regression Index formula automatically regresses Equal-parent indexes.

To use the Regression Index, one must know the breed or population average. This is something we think every breeder should know in order to more properly evaluate the standing of his own herd.

Various figures can be found which supposedly represent the various Dairy Cattle Breed Averages. We were not able to get categorical answers from all the breed secretaries as to the "average production of their respective breeds." From our study and correspondence, however, we could get the average butterfat test of the breeds. It seems that there is relatively little difference in the average yearly butterfat production of cows in the various breeds under similar conditions. This figure appears to be about 410 lb. of butterfat yearly for mature cows on twice-a-day milking under good Herd Improvement Test conditions. From the known butterfat tests and the assumed 410 lb. of butterfat we have constructed the figures shown in Table 49, which will have to do for the "Breed Averages" until the various breeds can supply us with the actual figures.

TABLE 49.—APPROXIMATE DAIRY CATTLE BREED AVERAGES

	Mature basis, 2×, 305 days		
	Milk	Test	Butterfat
Ayrshire	10,100	4.06	410
Brown Swiss	10,350	3.96	410
Guernsey	8,370	4.90	410
Holstein	11,550	3.55	410
Jersey	7,740	5.30	410

The figures in Table 49, it should be noted, assume that cows are milked for a full 305 days, twice a day, under good conditions. We realize that not all purebred herds reach the figures indicated in Table 49. Also, the basic figure of 410 lb. may be up to 5 per cent too much or too little for certain breeds. Until we can get more accurate figures from the breeds, however, the above approximate must suffice. Actually, the Ayrshire breed is now using the figure of 9,100 lb., which is the actual average for this breed, but this average includes many cows which do not milk the full 305 days. Those milking the full 10-month period approximate the figure shown in Table 49.

With the values shown in Table 49, one can compute Regression indexes for bulls in any breed. The chief advantage of the Regression

Index is that, knowing his breed average, the breeder can quickly arrive at a bull's apparent transmitting level. For example, if a Breed Average was actually 10,000 lb. of milk with a 4 per cent test and a bull of that breed is stated to have a Regression Index of 10,600 – 4.20%, we know immediately that his daughters produced 600 lb. more than normally expected (10,600 minus 10,000) and tested 0.20 better than normally expected (4.20 minus 4.00) regardless of the level of the dams to which he was mated. An Equal-parent Index of 10,600 milk and 4.20 test, on the other hand, could have been secured from dams 8,000, daughters 9,300—dams 14,000, daughters 12,300, and from millions of other combinations. The Equal-parent Index is not very revealing because it lacks any specific point of reference which the Regression Index has automatically in the Breed Average.

In addition, since the Regression Index moves very high or very low Equal-parent indexes halfway back to the Breed Average, its use in pedigrees and other advertising material would help to keep purchasers' hopes within reasonable bounds of possible accomplishment.

Bull Index as a Selection Tool.—Some people prefer to use the actual daughters' average as the measure of a bull's transmitting ability without standardizing the data even as far as age or number of milkings. In this form, we think the data practically worthless, at least so far as comparisons among bulls or prediction of future daughters are concerned. When standardized for age, number of milkings, and environment, if necessary and possible, the records of a bull's daughters are of great value in delineating his hereditary level of transmission. If the mates were a random average sample of the breed or population and the bull was later to be mated to a random average sample of the breed or population, such records are perhaps all that are necessary.

Some people standardize mates' and daughters' records and express the results as simple pluses or minuses for daughters in amount of milk, butterfat percentage, and total butterfat. This may be misleading because it fails to consider the normal average regression of 0.5 of groups of daughters on groups of dams. A bull bred to 6,000-lb. cows and having daughters at 8,000 lb. would show a 2,000+ figure, while one bred to cows averaging 14,000 lb. and having 12,000-lb. daughters would show a 2,000– figure, leading one to assign greater merit to the first bull. However, if the breed or population average was 10,000 lb., the normal regression of daughters on dams would call for exactly the figures secured, 8,000 and 12,000. In short, these two bulls are equal in transmission—both of them average rather than there being a spread of 4,000 lb. between them, as the 2,000 lb. plus and minus seem to indicate.

For more sound procedures in the selection of bulls, we need all the

breeding facts we can get and we need to use the facts as logically and completely as possible. To us this means using the standardized mates' and daughters' averages in the form of a bull index.

A bull's index is a numerical summation of standardized data from his mate's and his daughters' production figures aimed to express the bull's inherited level of transmission for milk, butterfat test, and total butterfat.

There are several factors which may limit the accuracy of an index.

Environment.—Since an index is based on the average production of a bull's mates and daughters, it is only as trustworthy as the records themselves. It is always possible that, either through design or chance, the mates or the daughters may have been more or less favorably circumstanced for high production than were their opposites. If this has happened, the index loses value. In assessing an index, it is necessary to establish the "normalcy" of conditions under which mates' and daughters' records were made and to make as reasonable an allowance as the facts seem to justify. Such allowances are arbitrary and may further distort rather than correct for differences. If the error is brought about by forcing a bull's daughters, the distortion will not be increased any more in an index than it would be in using daughters' records alone. If the distortion is brought about by lowering mates' production, the distortion will appear in the bull's index but would not in the daughters' average. One is, therefore, perhaps justified in discounting to some extent an index on a bull which was bred to very low record cows.

Since milk, test, and total fat are all elastic to some degree (some perhaps more than others), it is apparent that neither daughters' records alone nor an index can be infallible. Both of them are relatives, not absolutes. Since an index considers all the data, while the daughters' average considers only half or a little more of it, we prefer the index over daughters' records alone for the hereditary evaluation of a bull or as a prediction tool.

Genetic Interactions.—Another point which may influence the accuracy of an index grows out of the following facts: (1) the number of genes affecting milk, test, and total fat is probably large and (2) the genes probably interact with each other in a variety of ways other than in simply additive or multiplicative fashion to produce a given result (dominance or lack of it, epistatic effects, etc.) The practical breeder lumps all these and perhaps others into what he calls "nicking." This phenomenon is perhaps difficult of rigid proof, but many practical examples are most easily explained by recourse to "nicking," and the nature of the hereditary process would lead one a priori to expect it. If the early use of a certain bull in a certain herd does result in a favorable "nick," then the index derived from those early favorable matings may

be misleading so far as the results of the use of this bull on later cows of a different genetic background are concerned (and this would also be true of the use of his daughters' records alone).

Finagling.—Still a third factor may limit the accuracy of an index, namely, selection. Studies have shown that 5 daughter-dam pairs are a sufficient number on which to formulate an index, provided they are unselected daughters, although we personally still prefer to have at least 7 or 8 daughter-dam pairs (as does probably everyone else). If only the selected 5 best daughters (out of 10 or 20) are used in calculating the index, then the index is of very questionable value and adding more selected daughters would not help any. Selected daughters are invalid for indexing a bull; they are also invalid in themselves for estimating the genetic worth of a bull.

Unpublished data of Hyatt and Tyler of West Virginia on 473 Ayrshire sires with 17 to 20 or more tested daughters from tested dams showed the following regarding average butterfat production.

	Correlation	Regression of next 10 on 1st 7, 8, 9, or 10
1st 7 daughters and next 10 daughters	0.56	0.51
1st 8 daughters and next 10 daughters	0.58	0.55
1st 9 daughters and next 10 daughters	0.65	0.62
1st 10 daughters and next 10 daughters	0.65	0.62

These data also showed the following regarding Equal-parent Indexes.

	Correlation	Regression of index on next 10 on 1st 7, 8, 9 or 10
Index on 1st 7 and index on next 10	0.41	0.41
Index on 1st 8 and index on next 10	0.44	0.44
Index on 1st 9 and index on next 10	0.51	0.51
Index on 1st 10 and index on next 10	0.54	0.56

As Hyatt and Tyler point out, in this data the Regression Index on the 1st 7, 8, 9, or 10 daughter-dam pairs becomes the Equal-parent Index for the next 10. Apparently, if the first few daughters are above or below average, future groups of daughters will tend to regress toward the breed average and the same for indexes.

Then what answer can we give to the question, "What about indexes in the selection of bulls"?

To us the answer seems to be about as follows:

1. Since we want to know how good (or bad) a bull is as quickly and as completely as possible or on as few unselected daughters as possible, we can get the answer a little more quickly with indexes, since it requires about 50 per cent more total daughters to provide as valid an answer.

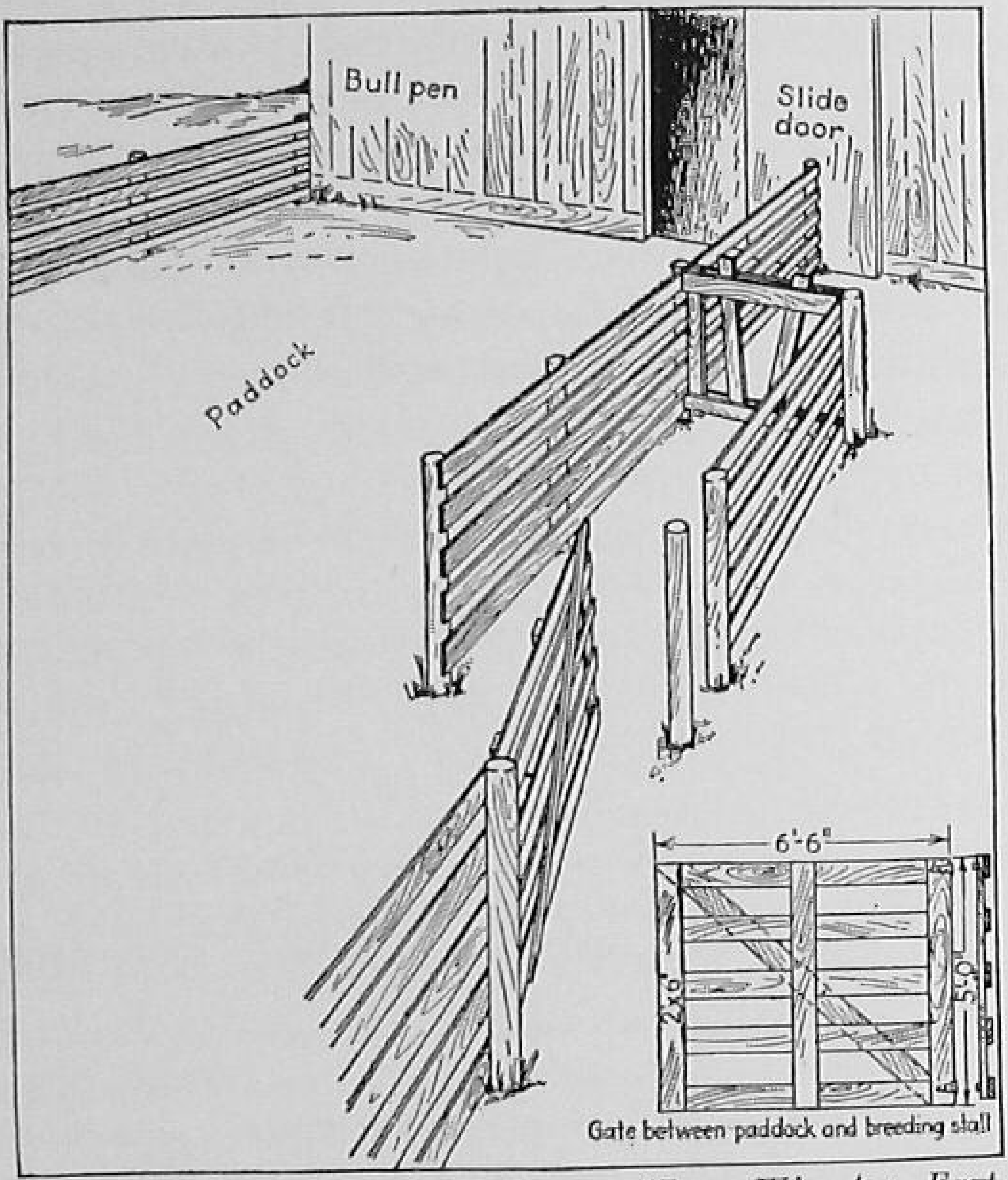


Fig. 176.—Any bull is "safe" in this sort of pen. (*From Wis. Agr. Expt. Sta. Cir.* 238.)

2. We must learn to take regression into account, to expect future groups of daughters beyond the first 7 to 10 to regress about halfway to the breed or population average. The Regression Index will help to reduce our hopes to somewhere near probable realization.
3. In artificial-breeding publicity, we should try to make our clients realize that:
   a. If the average of the indexes of the bulls being used in artificial breeding in any breed can be kept above the average of the cows of that breed in the area (or any given herd), reasonable progress in increasing production can be expected.

b. If a bull's first few daughters have done 450 lb. or his index is 500 lb., the client must not necessarily expect his own daughters by that sire to reach these levels. It depends on a lot of things—especially the genetic worth and perhaps specific genetic make-up of his cows and how he feeds and manages them. Better regress his hopes to some realizable level.

c. If a bull's Regression Index on his first 7 daughters is 450 lb. of butterfat, better use that as the Equal-parent Index for his next 10 or 100 daughters.

d. If a bull's index stands at 450 lb. and the cows he will be bred to average 400 lb., then the resulting 1,000 daughters will average about 425 lb. But that average means that there will be about 500 of them below 425 lb. Every artificial breeding patronizer will expect his neighbors to be housing and caring for these 500 below-average daughters. Many will probably want to "raise Ned" if they get one of them, so be prepared.

e. Because of the heterozygosity of our animals and the halving and sampling nature of inheritance, no one can predict with any accuracy what a certain daughter by a fairly indexed bull and out of a cow of known production will produce. An index on daughters' records is useful only in judging what future groups may do. The groups will inevitably show considerable variation, and there will probably be "squawks" from those on the lower side of average.

Age of Bull to Buy.—It seems fairly obvious that the best buy in a bull would be a proved sire, one that had already demonstrated his ability to transmit good type, production, and all the other desirable things which we want in a herd of dairy cattle. If the bull has done a good job of transmitting in one herd, he stands a good chance of doing likewise in another herd, but this is not an absolute certainty. Some bulls do well in one herd, not very well in some other herd, and the reverse of this occasionally happens too. If management is adequate in both herds concerned, the differing transmitting abilities of bulls is probably genetic. As the breeders say, the bull "nicked" well here, he didn't there. In other words, the genes of the bull fitted well with the genes of the cows of one herd but not with those of the other.

There are several difficulties with good adequately proved bulls: (1) There are not many of them; (2) their price is apt to be high; (3) they are often getting on in years and losing some of their breeding vigor and sureness; (4) they are often dead when we learn of them.

In other words, although good proved bulls are the best bet, few of us

are going to be apt to own them. Most of us, in other words, are going to be using young bulls for some time to come.

If we can't get a proved sire six or eight years old, should we buy a younger bull, say three or four years old? Some breeder may have such a bull and not want to use him on his own daughters but be anxious to keep him alive. If the bull has a good pedigree, if his daughters look good in comparison with their dams, if the herd is clean, so that we are not apt to be introducing disease into our herd by the use of this bull, and if he can be purchased at a reasonable price or, better still, leased at a nominal price, or if perhaps we find ourselves in a similar situation to this breeder we and the breeder might then just exchange bulls for 1 or 2 years, the bull problem would be solved for a while.

And so we might go on, all the way down to calves. A six- or eight-year-old bull might be proved, a four-year-old bull might have a group of yearling daughters, a two-year-old bull a bunch of calves being born, a yearling bull will have no offspring, but he has had a chance to grow out a bit so we can get an idea about what he is going to look like. With the calf, there is not much that we can determine perhaps except that he is alive and with good luck ought to remain so for some time.

There are dangers and possible disappointments in the purchase of any male. The problem is worthy of all the study and effort we can put into it.

The principal dangers with the purchase of older bulls are both physiological and genetic. In other words, the older bull used in some other herd may bring disease with him when he comes to us, and it is very easy to draw rather broad conclusions from rather few data. Perhaps a bull has half a dozen daughters that in their youth look a lot better than their dams which have seen a lot of hard service, but how will 30 of his daughters look 5 or 8 years from now? It is very easy to fool ourselves with a small number of young offspring.

With a bull calf, we generally largely avoid the matter of his introducing disease into our herd. Genetically, we can know nothing about him except what we can guess from his pedigree and his collateral relatives. The older bull gives us a chance to see a few of his offspring—generally too few and too young to be a very sure indication. The young bull, although having no offspring, is generally on the farm where he was bred. We, therefore, usually have a chance to study his sire and dam, often many other of their offspring and other direct or collateral relatives of the bull calf in question. Also the calf can usually be bought more cheaply.

There is no definite categorical answer to the question—is it better to buy a two- to four-year-old bull or a bull calf—provided a good, definitely

proved bull is not available. There are many angles from which the problem must be viewed, and the solution will vary with different individuals and circumstances.

One thing is certain, we need to prove more bulls. Records show that, on the average, out of every three bulls, one will give daughters that excel their dams in production, one bull's daughters will produce less than their dams, and one bull's daughters will produce at about the same level. When a young bull is purchased, he preferably should be used on 12 or 15 cows when he is just at or past a year old and then be leased, loaned, or just temporarily retired until 5 or 6 of his daughters have made records. In this way the good transmitting bulls can be discovered and, when discovered, used as extensively and as long as possible. The present system is generally the exact opposite of the above. A bull calf is purchased, he gets one to two crops of calves, and then he goes to the butcher to avoid inbreeding. Thus lots of good young bulls have been real "boloney" before their worth was realized, and by the same token, lots of poor bulls get by on the "phony boloney" of 6 or 8 good daughters out of a total crop of 60 or 80 daughters.

If a man is to be a successful breeder of dairy cattle, there are several "musts" in his program. We think the most important one of all is that he try out young bulls before putting them into heavy service. This, of course, is just another way of saying that to be successful, a breeder "must" use a series of good, proved sires.

Many breeders are solving their bull problem by joining artificial-breeding cooperatives, and the trend in this direction seems likely to continue, provided the sire selection committees of the artificial breeding cooperatives are able to do a thorough and painstaking job in the selection of proved sires and also in the matter of proving their own young sires.

Practical Shortcomings of the Progeny Test.—By means of the progeny test we can, it would seem, get a fairly definite idea as to the transmitting ability of a bull from a production standpoint. However, some practical considerations would indicate that even this method of breeding with bulls which have been tested by the progeny method and found desirable has serious shortcomings. In the first place, the method is expensive, because it implies the using of a one- or two-year-old bull on 12 or 15 cows and then setting the bull aside for a period of years and waiting to see how his daughters' milk yield compares with that of their dams. The gestation period in cattle is 9 months. The heifers are not bred until they are eighteen months old, then follows their gestation period of 9 months, and finally they must go through a 10 months' lactation period. This is at the very least a total of 48 months, or 4 years,

which must elapse after a bull reaches sexual maturity until his genetic make-up can be learned. Quite obviously such a procedure would never be put into practice except by an infinitesimally small number of the most affluent and farsighted breeders. In addition to the time and financial aspects involved in such a system of breeding only from proved sires, there is the additional fact that only a relatively small percentage of bulls would be proved good in any event.

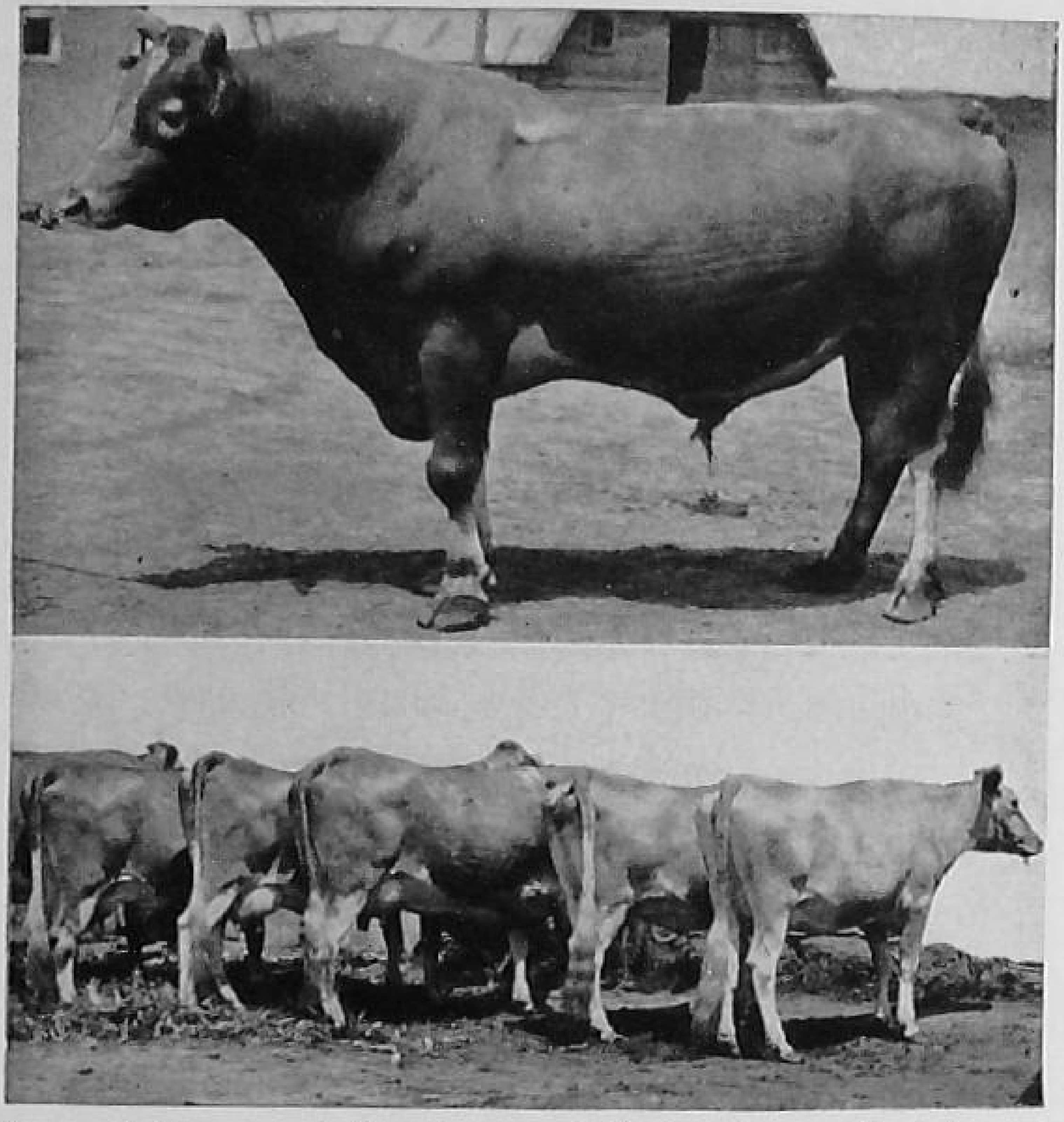


FIG. 177.—A proved Guernsey bull and some of his daughters. Ten dams averaged 333 lb of fat; 10 daughters averaged 533 lb of fat. (*Courtesy of W. D. Hoard & Sons Publishing Co.*)

Several state-wide inquiries in the United States have revealed that the average age of dairy bulls in service is about 2½ to 3½ years. Many dairymen will not keep an old bull because (1) of the danger involved, (2) of a wish to avoid inbreeding, and (3) of the danger of sterility.

Lush and Lacy have analyzed this problem in a very thorough-going way as the following quotation[1] will indicate.

Table 50 shows an estimate of the age distribution which might be expected among dairy bulls if the value of proven sires were so thoroughly appreciated

[1] LUSH, J. L., and LACY, M. D., The Ages of Breeding Cattle and the Possibility of Having Proved Sires, *Iowa Agr. Expt. Sta. Bul*, 290, 1932.

that every bull thought worth using in the first place was kept (unless natural causes of death or sterility interfered) until he could be proven and if all those proven to be distinctly better than the average of their breed were kept after the proving as long as they remained fertile and healthy. The figures in the table represent the maximum which could be attained in the direction of using as many proved sires as possible for dairy breeding. There are several rough approximations in the table, as for instance the estimate that during the first five years the losses from sterility and death from natural causes would only be a little more than 2.5 per cent per year and that after the bulls had passed 8 years, the losses from the same causes would run some 13 per cent per year and higher.

If these estimates are roughly correct, for every 1,000 bulls thought worth trying as sires in the first place, approximately 900 would go past 5 years of age and begin to be proven by the records of their daughters. Extensive data already collected[1] upon proven sires indicate that about one-third actually lower the production of the herds where they are used, another third do not change the production much one way or the other, and one-third produce distinct increases in the production of the herds where they are used. Therefore, it is likely that of the 900 bulls which begin to be proven between 5 and 6 years of age, it would rather quickly become apparent that about 300 of them were below the average merit of their breed and these would be discarded promptly. Of course the evidence would not all be available at once, and there would be many bulls about which the breeder would still be in doubt when they were 6 or 7 years of age. In Table 50, it is indicated that about half of the medium bulls would have their mediocrity definitely enough proven so that they would be discarded between the ages of 6 and 7 and the remaining half would be discarded the following year.

This would leave about 300 bulls which would be proven to be good and would still be alive at 8 years of age so that they would be available for further use. An annual loss of 30 or 40 each year through death and sterility from causes not under the breeder's control (only an estimate but probably not unduly high) furnishes the basis for the remaining figures in Table 50. When the figures in Table 50 are added, it is seen that there would be at any one time only 1,345 bulls 8 years of age or older which would be clearly proven to be superior sires among a total of 7,145 in use. This is not quite 20 per cent of the entire number of bulls in service. One thousand fifty more (those between 6 and 8 years of age) would be in the process of being proven and the very poorest sires would all have been discarded from this group. This would make a total under such nearly ideal conditions of about one-third of the sires in actual use which are either proven to be good or are partially proven and are indicated to be at least of average merit.

It becomes apparent, therefore, that, although the only method so far proposed for ascertaining the transmitting abilities of our dairy cattle, bulls especially, is scientifically sound, it has very practical limitations as

[1] McDowell, J. C., and Wintermeyer, W. E., Proved Dairy Sires, *U.S. Dept. Agr. Cir.* 3, September, 1927.

TABLE 50.—AGE DISTRIBUTION OF DAIRY SIRES ATTAINABLE IF ALL POSSIBLE EFFORTS WERE MADE TO PROVE SIRES AND TO USE AS LONG AS POSSIBLE THOSE PROVED GOOD

Steps in the proving process	Age of sire	No. of sires alive at this age	No. of sires that go out of service during year	Reason for decrease
5-year period before the daughters begin to prove the sires	1	1,000		Deaths and sterility from disease and accident
	2	975	25	
	3	950	25	
	4	925	25	
	5	900	25	
3-year period when proof is coming in and being culled accordingly	6	600	300	Disease and accident plus the culling of ⅓ which prove to be distinctly inferior. Further culling of ½ those proved mediocre
	7	450	150	
	8	300	150	Culling of the remaining mediocre ones
Period after proof is complete and only the distinctly superior sires are kept	9	260	40	Deaths and sterility from disease and accident
	10	220	40	
	11	180	40	
	12	145	35	
	13	110	35	
	14	75	35	
	15	40	35	
	16	15	25	

far as expediting the creation of a more beautiful and more efficient population of dairy cows.

Selecting a Young Bull.—If one cannot or does not desire to buy an older bull, does not choose to use bulls standing at artificial-breeding units (and if everyone used these bulls and demanded that his cows be bred to proved sires, there would be no one left to try out young sires to find the good ones and dairy-cattle breeding would be in for a tumble), then he must gamble on a bull calf which he must select on type and pedigree.

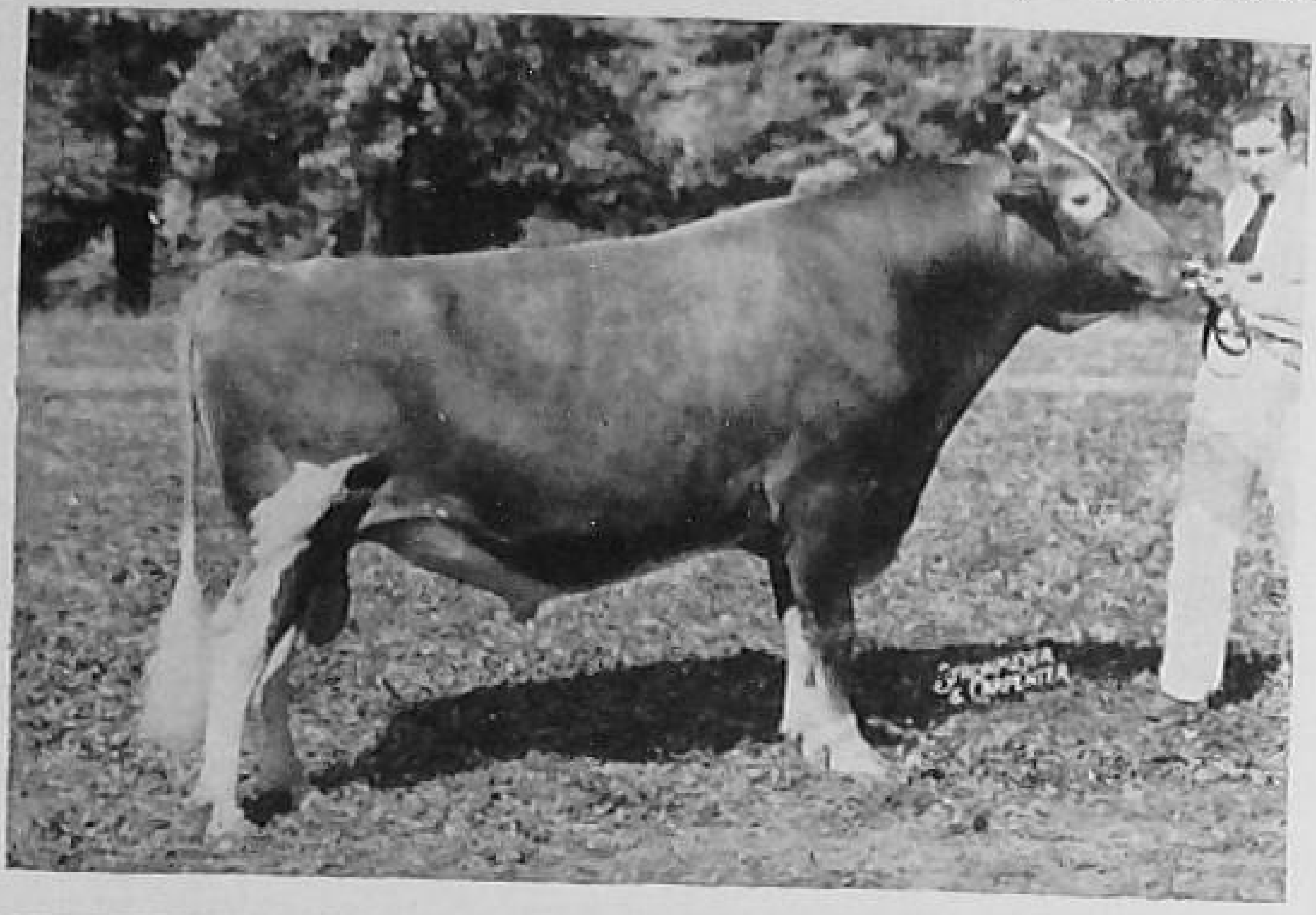
There has never been proved to be a best type for dairy bulls. There is an accepted show-ring type, and the purebred breeder must perhaps pay some attention to it. How much harm this has accounted for over the past 100 years, it is impossible to say. There is but a small correlation between type and production in cows. There is a very small

correlation between type of dam and type of daughter. There is probably no correlation between type of dam and production of daughter and no correlation between type of sire and production of daughter. Then why pay any attention to type in a bull? We do not know the answer. We have often thought, however, that the dairy industry might move ahead faster if type in bulls was given no standing and no bulls were shown at fairs and expositions. We do not know what influence great show bulls have had on the various breeds either in type or production. We seriously doubt whether the good they may have done outweighs the bad in either category, and we believe further that production might move ahead faster if breeders could give only such consideration to type in bulls as they choose of their own free will to give. We asume they would give some, but perhaps not as much as they now feel they must. Having to pay so much attention to type in bulls means that other more important things can get less attention, and selection is, therefore, not so effective as it otherwise would be. In selecting a wife (assuming man does the selecting), we would have a fairly wide choice if we demanded only a certain minimum of physical charm. If in addition we say, "She must also be a good cook," our choice is narrowed. If we also stipulate that "she" must have a million dollars, our choice practically vanishes, assuming that there is no positive correlation among these things but, as is more likely, a negative one.

In production we have a little more solid ground on which to stand and can say something positive without too many *if*'s, *and*'s, and *but*'s. The most important feature about a young bull is that he be the son of a good proved sire, the latter animal being one whose Regression Index for milk and test are above the breed average (the farther above the better), whose sons are bulls with good indexes, and whose offspring are of acceptable type. We say this because we have found a good correlation between size of index of sire and size of index of sons in several breeds; *e.g.*, 569 sons listed in Volume 15 of the *Holstein-Friesian Red Book* show a total production 4 per cent fat-corrected milk correlation with their sires of $+0.31 \pm 0.03$ and a regression of $+0.38$. Like father, like son to a considerable extent.

If the sire (call him A) of our young bull is a proved sire, this means that he has daughters with records out of dams with records. We next would group these records to see whether bull A "nicked" any better when mated to the daughters of certain bulls. If study showed that he had "nicked" better when mated to daughters of bull F, then bull F, if a bull proved good through his sons and daughters, is elected as maternal grandsire of our young bull. Study of bull F might reveal that he had done best when mated to daughters of bull M, which places bull M,

if a good proved sire, as the maternal great-grandsire of our young bull. This gives us the three sires on the bottom line of the pedigree of our proposed young bull. Now we must find a good daughter of bull M, a cow with several good records and several good offspring to be the maternal



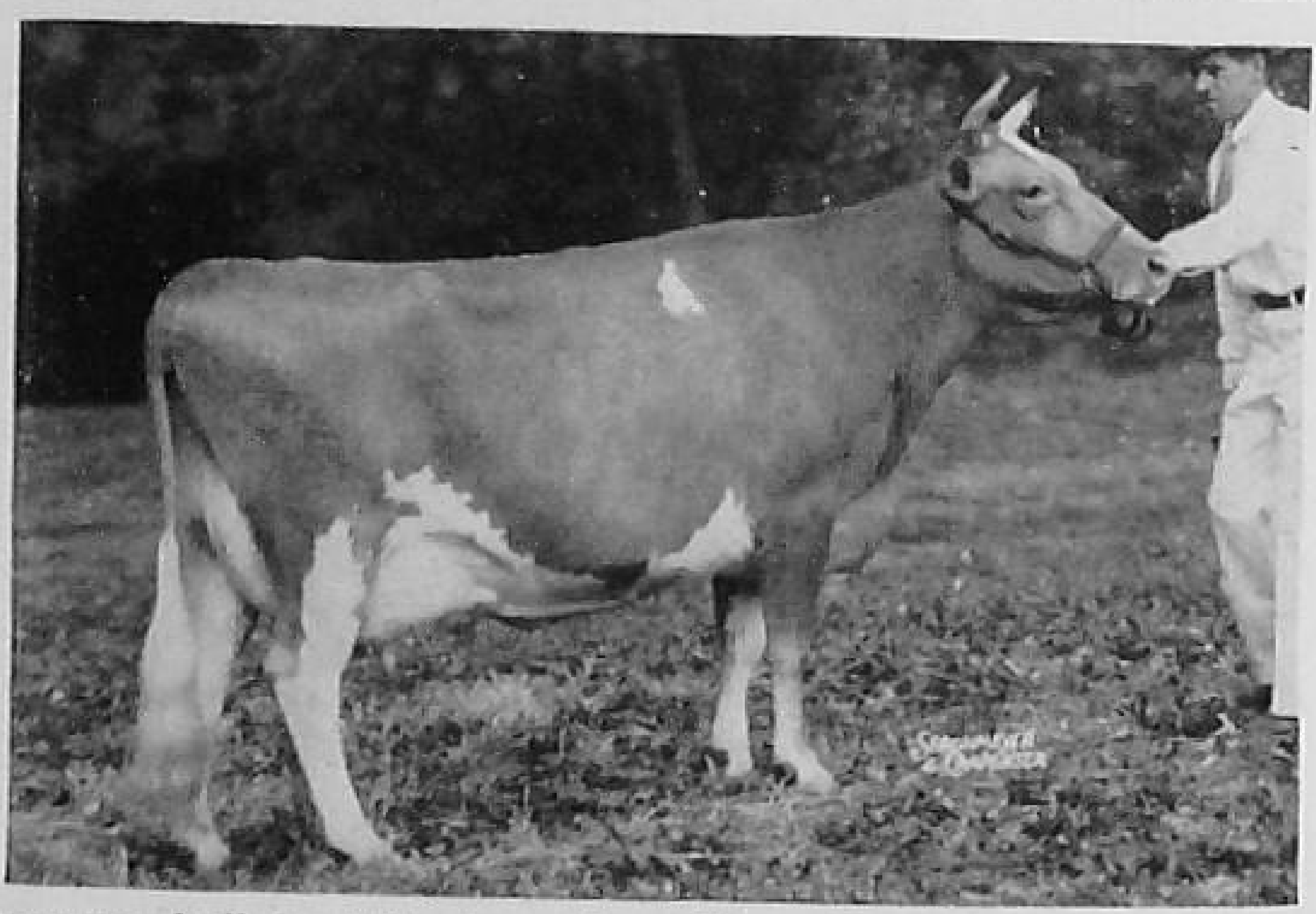


FIG. 178.—Guernsey bull (*top*) Cowham Farm Tress King, first-prize bull, three years and over, and senior and grand champion, winner of the Langwater Trophy. Sire: Riegeldale King's Philosopher. Dam: Rex's Tress of Cowham Farm. Breeder and owner: C. F. Cowham, Jackson, Mich. Cow (*bottom*) Adohr Eldor Pearlette, first-prize female, five years and over, and senior and grand champion. "Pearlette" won the Douglaston Manor Farm Trophy for best AR cow, the Meadow Lodge Farm Trophy for best uddered cow, and her breeder was the winner of the Guernsey Island Perpetual Challenge Trophy. Sire: Eldor of Adohr Farm. Dam: Escalon Pearlette. Breeder: Adohr Milk Farms, Tarzana, Calif. Owner: Adohr Farms—Merritt H. and Rhoda R. Adamson, Carmarillo, Calif. (*Courtesy of American Guernsey Cattle Club.*)

granddam (call her Y) of our young bull, and finally we must find a good daughter of bull F and out of cow Y, a cow we will call X who has several good records and several good daughters, and she will be the dam of our young bull. This procedure is not theoretical; *i.e.*, it is practical. One

might ask, "Where would one find that kind of situation?" The answer is in any good herd which has used three good sires in succession. They first used bull M and got a lot of his daughters. These were bred to bull F to get a lot of his daughters. They are now using the good proved sire A. In such a herd, if of fair size, there would be considerable choice of cow family—of what we designated as cows Y and X. Not all bulls selected in this way will turn out to be good ones, but four out of five of them should. Since inheritance is a halving and sampling process, there is no way to take all the guess out of breeding.

We have applied our thinking in the above example to production. We could also apply it to type, so that if we picked a young bull of acceptable type whose pedigree, analyzed for type as favorably as we have just demanded it analyzed for production, we would, no doubt, have a young bull which would sire good type.

Up to the present, a good proved sire has meant one whose daughters have done well considering the level of the dams to which he was mated. Proved bulls have been valued very highly especially by artificial-breeding associations. This has created the temptation to try to make bulls look as good as possible. Perhaps there has been some cheating—feeding and managing dams on a much lower plane than daughters. Such manipulations are easily possible, and there may now, or in the future, be mediocre or poor bulls masquerading under rather high indexes.

A further and more definite check on the probable genotypes of bulls consists of studying how their sons perform. Daughters in one herd can be manipulated to give apparently good results. Sons scattered over several herds could not be juggled so easily. A bull can be proved through his daughters when he is five or six years old. To prove him through his sons will take about 2 years longer.

We think one good way to spot good bull prospects is to watch for those bulls in any breed which begin to show up with good sons. If the first few sons of a bull to become proved really look good, then we could write to the breed association and get a list of all his registered sons and perhaps find a few out of good cow families which might merit a trip to study their offspring. In this way, we might find a good four- or five-year-old son of a good proved sire (out of a good cow in a good cow family) who, while not yet proved, will be in another year or two. If the first few sons of a bull prove out well, it seems probable that more will later. Studies do indicate that later sons of proved sires will not be so good or so poor as earlier ones—will tend to regress toward the breed average, but this is a possible source of bulls which has not been utilized as much as it might be with advantage. Cow family must be scrutinized

very carefully when using it, however, because early sons are likely to be out of good cow families, but when the older bull begins to get a reputation through his sons, it will be a temptation to the breeder to sell his sons out of any old cows.

Another possible source of good herd sires is to induce the owner of a well-proved sire to breed said sire back to a few of his own best daughters. If we can get a calf bred that way, he will have 75 per cent the same genes as his proved sire.

In the past, most breeders have used a good bull or two, then a poor bull or two, etc., which, together with the fact that within-herd heifer selection has not been very soundly based, means that genetic improve-

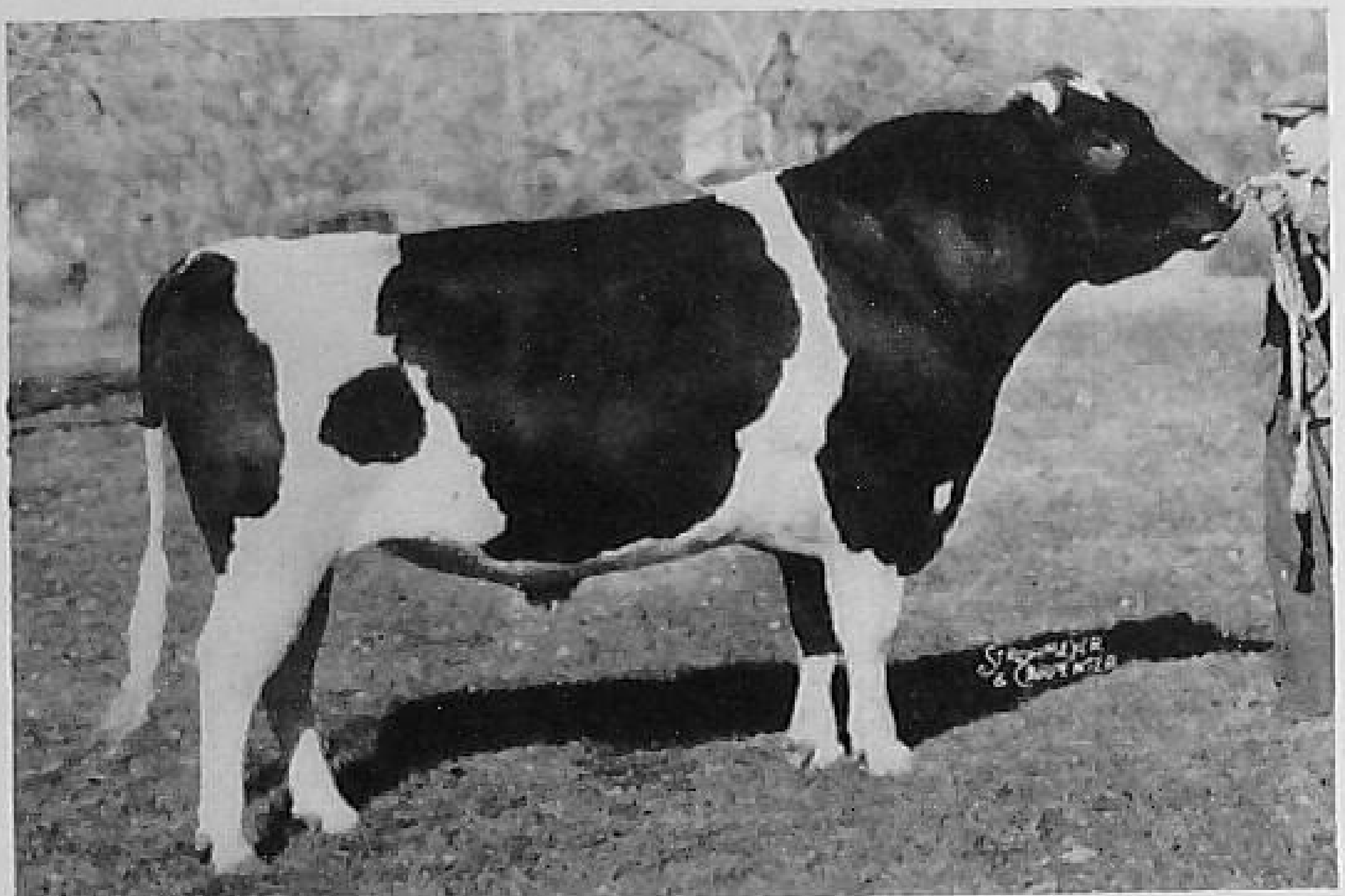


FIG. 179.—Sir Bess Ormsby May 2nd, a great Holstein sire—result of mating of daughter back to her sire, Sir Bess Ormsby May. *(Courtesy of Mrs. W. S. Kellogg.)*

ment in dairy cattle has been very halting. If the last three bulls which a breeder has used have been good ones, then that breeder now has a good herd. We often say that the place to buy your next bull is at some farm where the last three bulls used have been good ones, and then we get off onto another topic before anyone has time to ask us the location of such farms and, speaking seriously, they are rather few and far between.

Bull Transmitting Chart.—The art of animal photography has made rapid progress during the last 20 or 30 years. To bring out photographically the best points of an animal and to minimize the weaker ones is a very difficult procedure and one requiring an infinite amount of patience and practice. When the job has been well done, however, it has decided limitations from a breeding or selection standpoint, because the photograph portrays only the phenotypic aspects of the animal. In addition, the breeder also needs some method of getting a picture of the animal that will portray his or her genotypic aspects.

The following graphs are an attempt to supply this need, especially for production.

Figure 180 shows a graph for the Holstein bull, King of the Ormsbys, in regard to amount of milk. The 84 cows to which this bull was mated were grouped according to production to the nearest 1,000 lb. The solid line of the graph shows that there was one cow in the 12,000-lb. class, one in the 13,000-lb. class, two in the 14,000-lb. class, three in the 15,000-lb. class, etc. The broken line of the graph shows that out of these 84 cows, this bull sired three daughters in the 15,000-lb. class, three

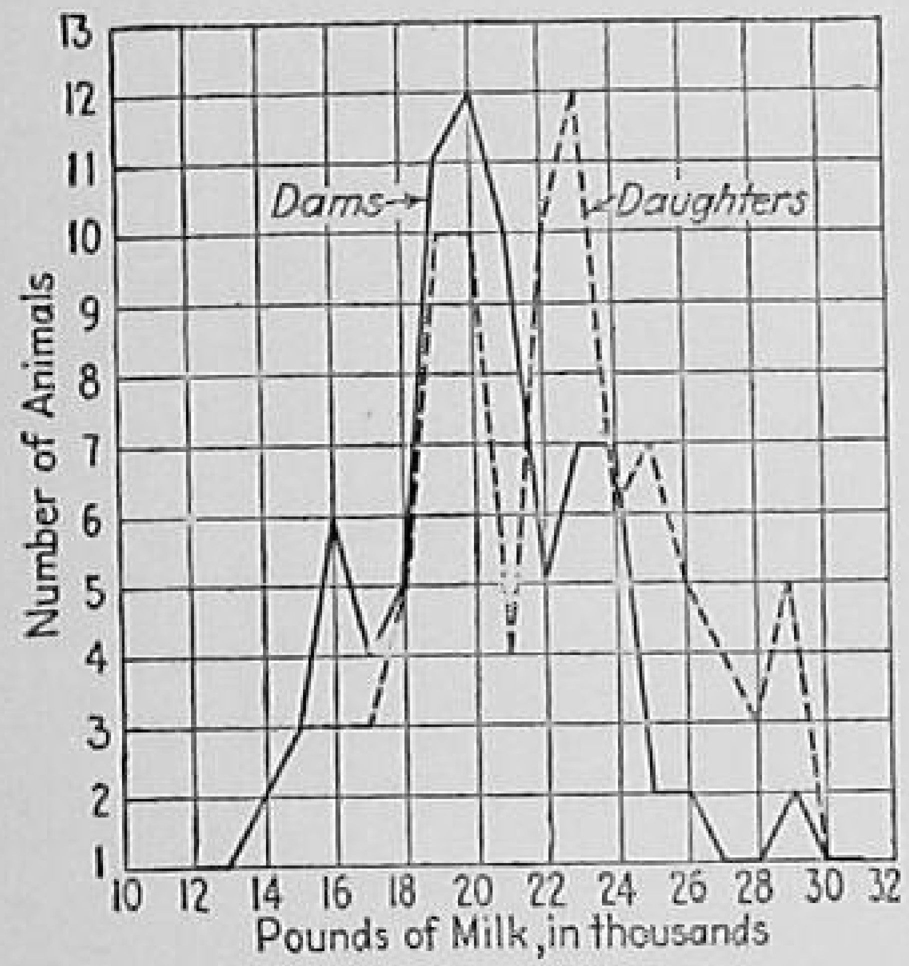


FIG. 180.—Daughter-dam chart for the Holstein bull, King of the Ormsbys.

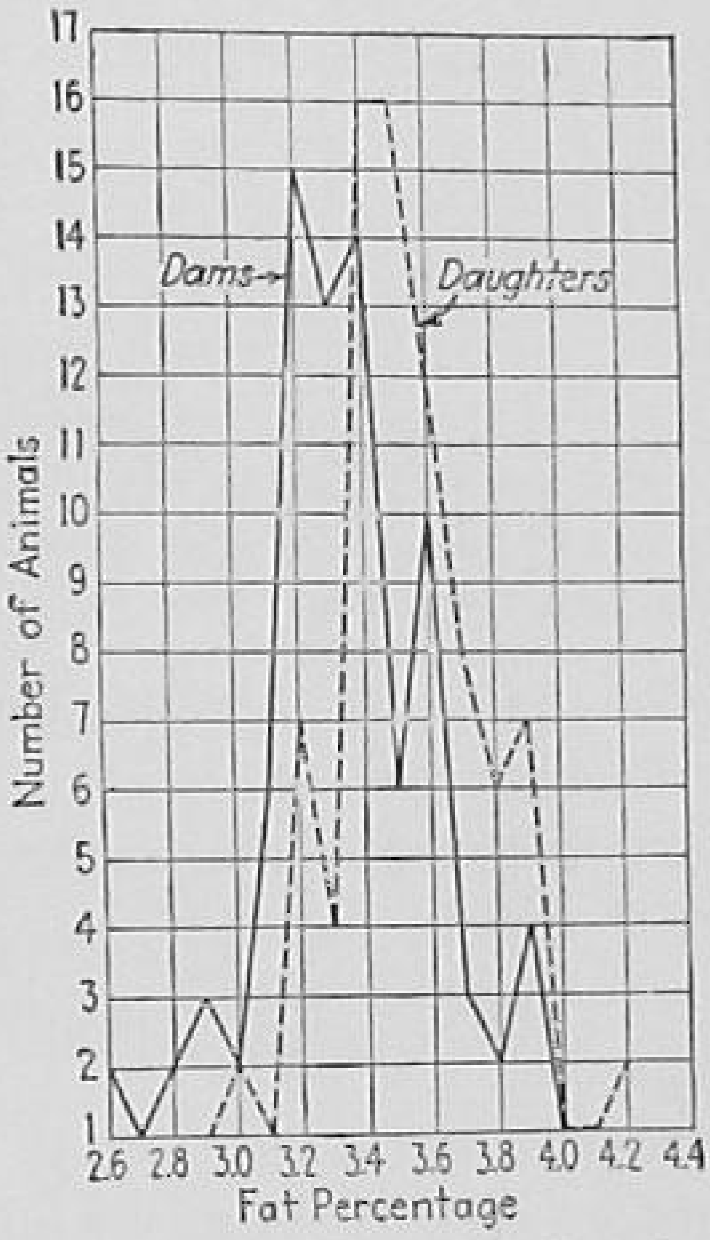


FIG. 181.—Daughter-dam chart for the Holstein bull, King of the Ormsbys.

daughters in the 17,000-lb. class, five in the 18,000-lb. class, etc. The dams' mean was 20,547 lb. and the daughters' mean 22,190 lb. The standard deviation of the dams was 3,858 lb. and that of the daughters 3,465 lb., and the coefficient of variation of the dams was 18.8 per cent and the daughters 15.6 per cent.

A desirable bull is, of course, one who moves the mean to the right; *i.e.*, increases average production and also lowers the coefficient of variation. If a bull is able to do both these things, it indicates that he is more or less homozygous for the genes making for high production. This sort of graph, in other words, presents a picture of the genotypic make-up of this bull, which shows at a glance just what sort of breeder he is.

Figure 181 shows in the same manner the genotypic make-up of this bull from the standpoint of fat percentage. In this case the dams' mean was 3.34 per cent, their standard deviation was 0.288 per cent, and their coefficient of variation 8.62 per cent. The daughters' mean was 3.54 per cent, their standard deviation was 0.256 per cent, and their coefficient of variation 7.23 per cent.

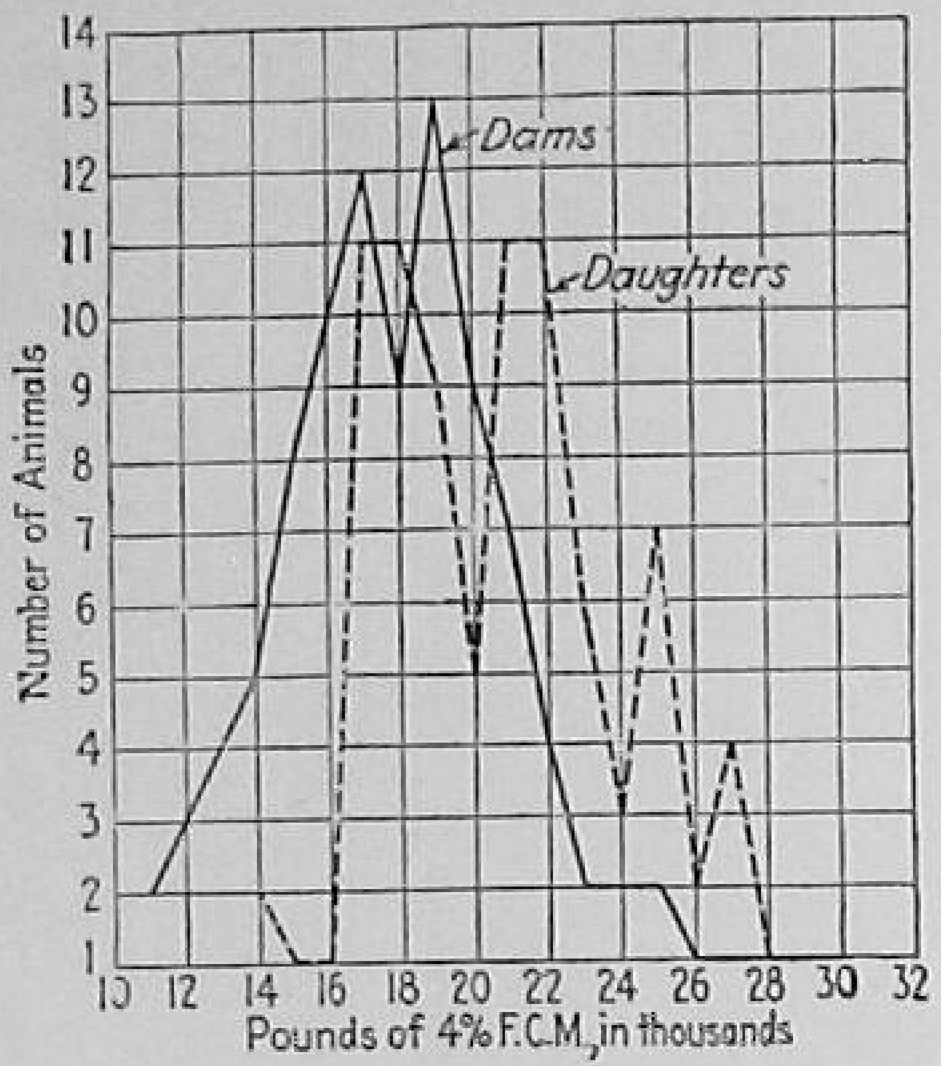


FIG. 182.—Daughter-dam chart for the Holstein bull, King of the Ormsbys.

Figure 182 shows a graph for this same bull on the basis of 4 per cent F.C.M. The coefficient of correlation between dams' and daughters' production on a 4 per cent F.C.M. basis was also calculated and found to be a positive correlation of 0.57 ± 0.04, indicating that the level of production of these dams did influence considerably the level of production of their daughters, which adds weight to the argument for using both dams' and daughters' records in computing indexes for bulls.

Herd Knowledge and Heifer Selection.—A breeder must start from where he now is, with whatever heredity is now present in his herd. He will hope to gradually improve the inheritance in his herd—primarily through the use of better sires. Obviously his first task is to learn more completely what he has.

Since he is going to pay some attention to type, that would be a good place to start. He could arrange to have his herd classified, and by assigning values of 95 for Excellent, 87.5 for Very Good, 82.5 for Good Plus, 77.5 for Good, 72.5 for Fair, and 67.5 for Poor ratings by the official classifier, he could work up the average score for his own herd in general appearance, dairy character, body capacity, mammary system, and over-all rating. The breeder must go into type matters much more thoroughly than this, however. He must know whether his animals are good- or plain-headed, fine- or heavy-shouldered, strong- or weak-topped, wide- and level- or narrow- and peaked-rumped, straight- and strong- or crooked- and weak-legged, and especially about any general weaknesses in size, quality, contour, and attachments of udder and teat placing. Only with thorough, detailed, and clear-cut knowledge of his own present status can a breeder be fully armed to start the search for his next sire. Breeders can work up the data on their own herds, students on their college or school herd, and this type of study must be both

No.________ Record Card for Each Cow Breed________

Name________

Breeder________

Date of Birth________

Weight at Maturity________

Picture

Records

Length of Record	Number Milk-ings	Age at Start	Total Production Milk	Total Production Test	Total Production Fat	305 C Mature Milk	305 C Mature Test	305 C Mature Fat

Daughter's Records 305 C Mature

Name	No.	Milk	Test	Fat

Date Bred	Bred To	Date Calved	Length Gestation	Sex of Calf	Remarks	What became of calf

FIG. 183.—Record card for use in dairy herd (*see other side*).

Pedigree__________

Sire__________

Index:

Grandsire__________

Grandam__________

Dam__________

Ave. Record (305 C Mature):

Grandsire__________

Grandam__________

Other Remarks

Type

Ease of milking

Persistency

Heat periods

Remarks:__________

Health Record

T.B. Test__________

C.A. Test__________

Mastitis__________

Other Troubles__________

Sold at_____years of age because__________

Fig. 183.—Record card for use in dairy herd.—(*Continued*).

thorough and critical. Presumably the next sire is going to begin to correct the present herd faults; but before he can be intelligently chosen, both as to individuality and family, the herd faults must be crystal clear in the breeder's mind.

Improving our dairy cattle depends primarily upon our being able to recognize the cows which are genetically in the upper half of the normal distribution curve and to get them bred to genetic upper half males. Since the heritability of type and production runs somewhere up to 30 per cent, it is obvious that while selection from good-type, high producers would move us ahead, our rate of progress would be slow because we would be building our hopes on a great deal of favorable-looking variation which was not caused by additive genetic factors but by other types of genetic interactions and by the environment. Genetic variations other than additive may be partially captured, but environmentally caused variations, not at all. It is plain for all to see, therefore, that the dairy-cattle breeder must get more factual data on the animals in his herd, must organize the material into its most readily usable and most valuable form, and plan his matings with a view to strengthening weak spots and intensifying the good qualities he seeks if he is to hope to make any real progress in his all-too-short lifetime.

Figure 183 is a sample record card for use in a purebred herd. A sheet (this or a similar one) should be made out for each cow and kept up to date at all times. The reason for this statement is twofold: (1) the limited storage capacity of any brain, (2) the absolute necessity for getting production and reproduction facts out where we can see them and use them.

In our opinion there is only one best way to determine what cows to save heifers from, namely, their own type and performance and their family. If heritability of desirable things in dairy cows were high, we could select from our better individuals and let it go at that. Heritabilities for the things we want are generally low, which means that it will pay to consider family as well as the individual cow in deciding which cows to save heifers from.

We described in the previous chapter how a herd could be set up into its respective cow families. It takes a little time to do this; but when once done, cow-family charts can be kept up to date with very little effort—adding the new heifers when born and reaveraging the production performance for living cows whenever they complete a new 305-day period, or once a year. When records have been kept for a few years, it will be possible to set the whole herd up graphically, as is illustrated in Fig. 184; and when this can be done, the breeder can eliminate a consideration of the retention of certain calves as replacements even before

they are born, because they are in poor families which he is planning to eliminate gradually from his herd. Then he can devote his whole attention to choosing the better calves in the better families to serve as replacements.

Likewise, the task of choosing a bull calf from another breeder's herd will be greatly simplified when the breeder can display a chart of his whole herd as indicated in Fig. 184. We may hear of a breeder with a good proved bull and decide we would like a son of this bull. We go to

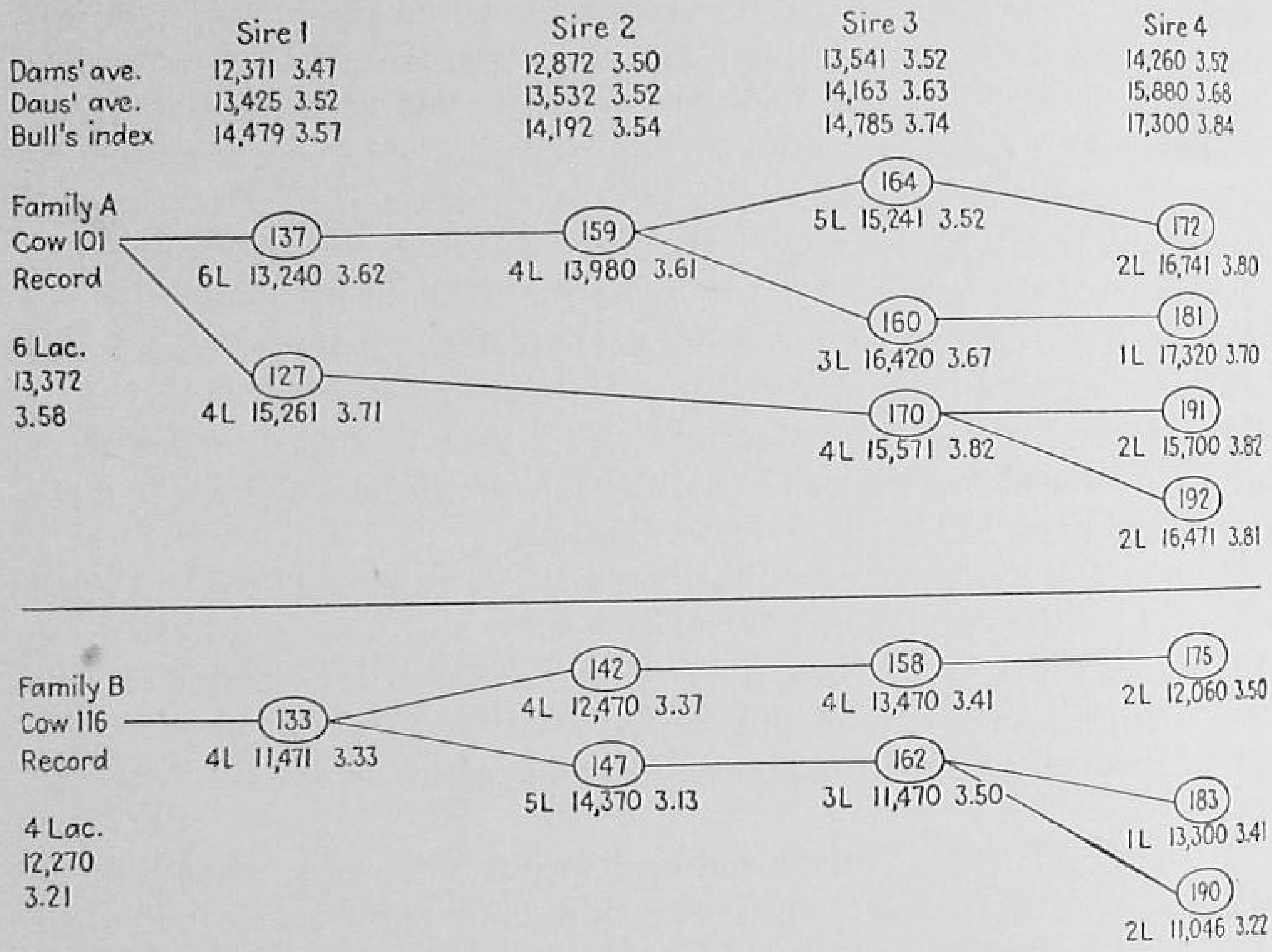


FIG. 184.—Two cow families of very different breeding worth.

this farm and study the female lines as charted and try to pick our bull calf from a good female line, one in which each generation of females has proved to be better than the dams. We find from the chart two or three cows meeting this requirement, and then we go out to the barn to make our choice between these calves on the basis of their own and their close relatives' individualities. Such a scheme of selection gives a double check. We not only get a son of a good proved bull, but we secure him from a line of females that has shown steady progress generation by generation.

Two cow families are shown in Fig. 184. Family A is a good one, family B not so good. The chart is to be read in the following manner. Foundation cow 101 had 2 daughters by sire 1; one (137) averaged

in 6 lactations 13,240 lb. of milk testing 3.62; the other (127) averaged 15,261 lb. of milk testing 3.71 in four lactations. In family B, foundation cow 116 had a daughter by sire 1 that averaged in four lactations 11,431 lb. of milk testing 3.33. The daughter 137 of foundation cow 101 by sire 1 in turn left a daughter (159) by sire 2 that averaged in four lactations 13,980 lb. of milk testing 3.61; whereas the daughter (133) of foundation cow 116 by sire 1 left 2 daughters by sire 2, one of which averaged in four lactations 12,470 lb. of milk testing 3.37; and the other (147) averaged in five lactations 14,370 lb. of milk testing 3.13, etc., through the rest of the chart. All the descendants of foundation cow 101 (there were 20 in all) averaged to produce 16,020 lb. of milk testing 3.75, and all the descendants of foundation cow 116 (13 in all) averaged to produce 12,340 lb. of milk testing 3.34 per cent.

It is obvious that from a production standpoint selection in family B should be stopped and selection of replacements confined to family A, with due attention given to type, longevity, ease of milking, freedom from disease, regularity of breeding, etc. If a breeder keeps records, he can analyze his herd in the above fashion, and only then is he in a position to select his female replacements intelligently. If he does this and uses care in the selection of his sires, there is no reason why he cannot make progress in building up a higher producing herd. Records provide the only intelligent basis for the art of selection.

One possible way to lump together the effects of inherent producing capacity with regularity of breeding, freedom from disease, etc., is to compute the average daily production for each cow from the day they freshen as heifers until they leave the herd. This simply means dividing a cow's lifetime production (standardized to a 4 per cent F.C.M. or particular breed basis) by the number of days she remained in the herd following her first calving. If she had high inherent milk-producing capacity and persistency and dropped a calf on about the same day each year for a number of years, her average daily milk production (milking days and dry days) will be high. The dairy farmer prospers or not depending on the average daily production of all the cows in his herd, so this figure for each cow and for each cow family can be very useful in guiding selection.

Some breeders find it difficult to think in terms of cow families arranged as in Fig. 184 where we start at the left and read to the right in order to go from ancestors to offspring, whereas in a pedigree we move from right to left as age decreases. The material in Fig. 184 can be shown as a pedigree if one wishes by simply listing all the off-spring of the females on the bottom line of the pedigree.

Because of the limitations of space, we have shown only the lines

with living descendants and nothing but the records in the cow-family chart, Fig. 184. The breeder should also list on his family charts all pertinent data concerning the animals in each family, *e.g.*, the type, mature weight, number of services per conception, abortions, mastitis, difficult calvings, average time between calves, and then work up the averages for each family.

All sorts of things, both good and bad, run in cow families; *i.e.*, they are more likely to be found in this family than they are in that one. Here is a family which averages 16,020 lb. of milk with a 3.75 test over an average of 5.6 lactations per cow, has a type score of 83.2, requires 1.83 services per conception, is seldom bothered with mastitis or abortion.

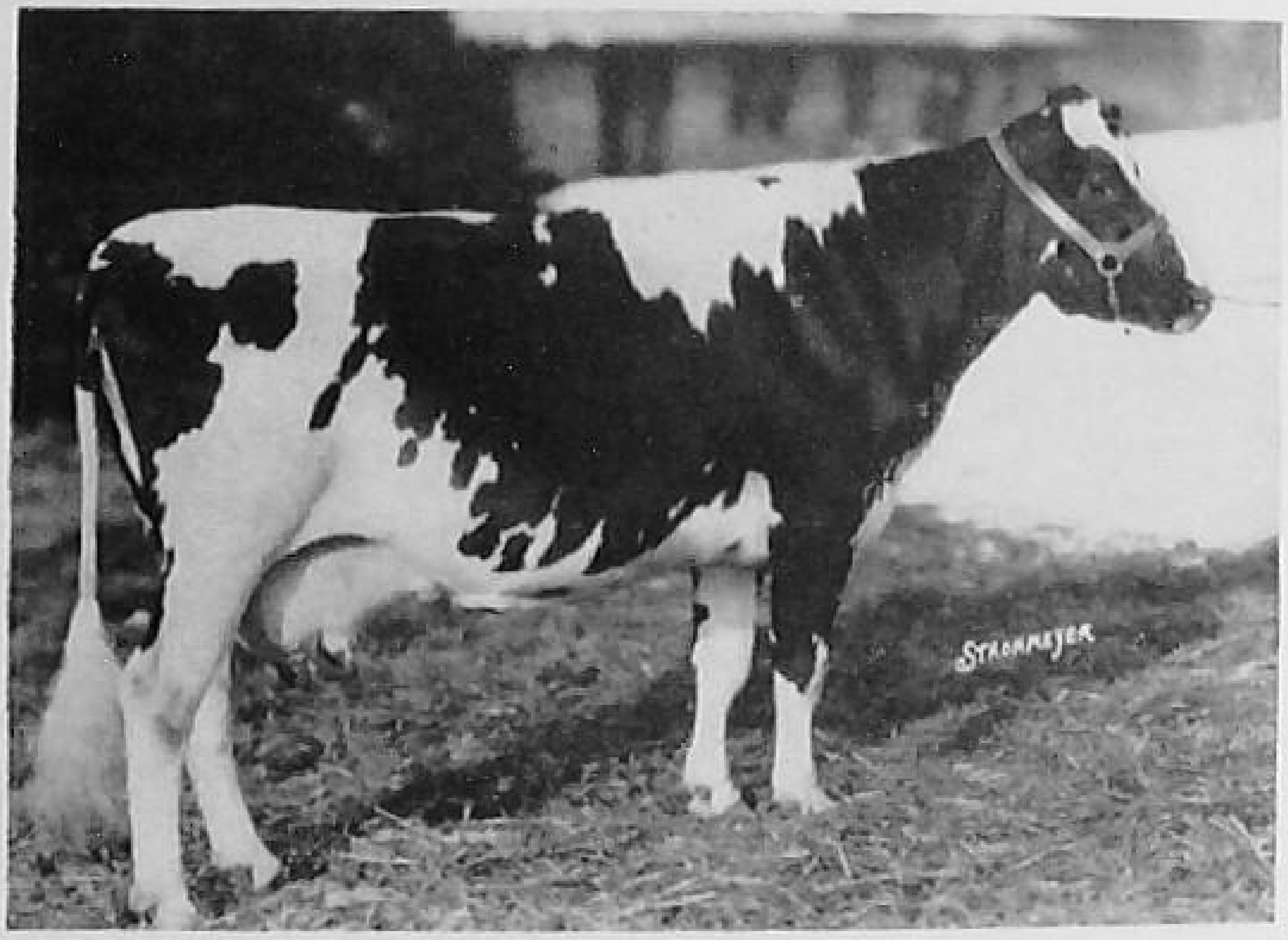


Fig. 185.—Countess Chloe, foundation cow to which more than 90 per cent of the Holsteins at the University of Massachusetts now trace on the bottom line of their pedigrees.

Another family averages 12,340 lb. of milk with a 3.34 test over an average of 3.1 lactations per cow, has a type score of 80.1, requires 2.21 services per conception, and is bothered a lot with mastitis and with "casting the withers" a frequent accompaniment to calving. The breeder's first job is to analyze his herd, know his best cow families and broaden the base of his selection (make it more foolproof) by paying attention to family, which is a better guide to genotype, especially in young animals, than is their own individuality or phenotype.

It is genetically unsound to select dairy heifers solely on the phenotype of their dams. It is not strange for a good phenotype to appear occasionally in a poor family. It is very questionable whether her offspring should be saved. Speaking generally, it would probably be better to save from a less good phenotype in a good family than from a better phenotype in a poor family. Ideally, of course, we should save from

good phenotypes in good families, the close relatives or family serving to fill in many of the blanks which the animal's own phenotype can shed little light on. If she is a young cow without any or with only one record, many pertinent questions cannot be answered directly—will she be a regular breeder? resistant to mastitis? long-lived? a consistent producer? etc. Time alone can supply the final and complete answers to these questions. But if the cow-family chart shows that all her close relatives have performed well in these various regards, the chances are certainly greater that the present young cow will follow this family pattern.

The most necessary lesson for American breeders to learn is that of thinking in terms of *family groups*. We have analyzed many herds of

FIG. 186.—Holstein bull, Clovercourt Ormsby Royal Blend, a ten-year-old bull which has sired over 17,000 offspring in the New York Artificial Breeding Cooperative. (*Courtesy of S. J. Brownell, Cornell University.*)

dairy cattle and arranged the animals into their respective cow families. Without exception we have found breeders saving as many or more heifers from their poorer cow families as they were from their better ones. Good and bad hereditary traits do run in families, and there is ample justification for the old Scot's admonition to his son, "Sandy, never marry the only good girl in a family." What animal breeding most needs is to put a broader base (than individuality) under selection. The best way to do this is to arrange one's herd into its female lines and consider family along with individuality.

Actually we have not used individuality or phenotype very intelligently. We are likely to take a cow's highest record as the measure of her genotype. This is unsound because so many environmental happenstances can make a record large or small. Lush, from a study of repeatability of cow's records, arrived at a figure of 0.4 for the usual run of

herds (higher possibly where environment has been well standardized and corrected for). Since each performance of any trait yields additional information although on a decreasing scale, Lush suggests the following formula (based on repeatability of 0.4) for arriving at a cow's ability, $\frac{2n}{2n+3}$ times her own average plus $\frac{3}{2n+3}$ times the herd average, n standing for the number of records. Therefore we can broaden the base of selection based on individuality by properly weighting many performances into an average.

We can widen it still further by considering close relatives along with the individual's phenotype. The current herd average can perhaps best serve as a point of reference. If a breeder's herd average is now 450 lb. of butterfat, he can rate each cow by summating the following:

difference between cow's own average and herd average + or −
0.5 difference between her sire's Regression Index and herd average + or −
0.5 difference between her dam's average and herd average + or −
0.5 difference between her daughter's average and herd average + or −
0.5 difference between her full sister's average and herd average + or −
0.25 difference between her maternal grandsire's index and herd average + or −
0.25 difference between her maternal granddam's average and herd average + or −
0.25 difference between her half sister's average and herd average + or −
0.12½ difference between her aunt's and uncle's performance and herd average + or −

This sum + or − is added to the herd average in order to get a more accurate estimate of each cow's genetic or breeding merit than her own record alone can provide. In this way all the females in the herd can be listed in the relative order of their merit. It must be understood that this figure is relative, not absolute. If we know a dam's performance through several records, we do not learn as much additional from her parents as the above figures indicate. It is just a rough way of gathering together the data from close relatives to give a somewhat more accurate measure of an animal's probable genotype than her own phenotype itself can yield. Type and other qualities considered important by the breeder can be treated in similar fashion.

We cannot see the genes in the chromosomes of our dairy cattle—we probably would learn nothing if we could, because it seems unlikely that they bear any labels as to what they are or do. By keeping records,

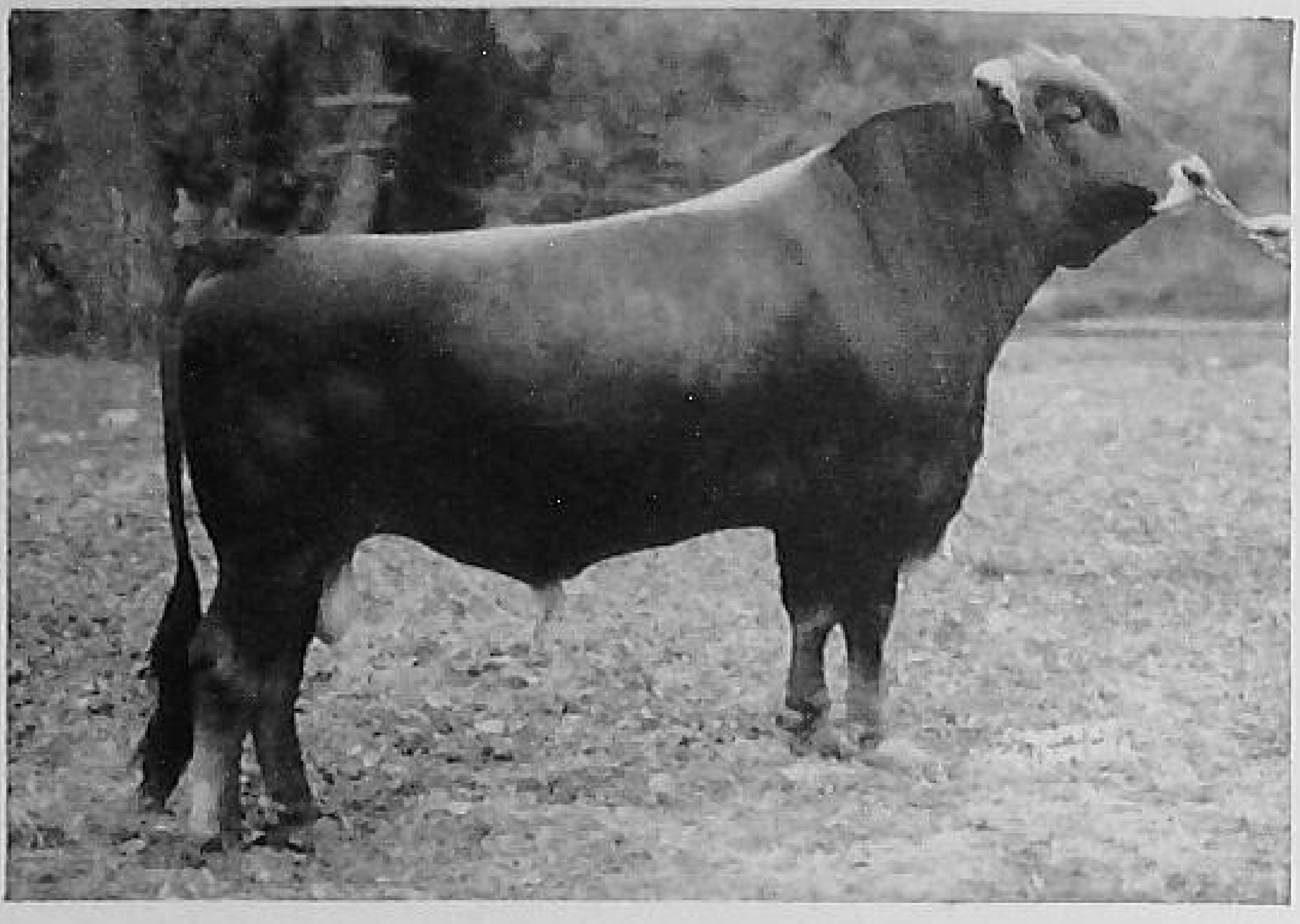
the breeder can begin to get some notions as to the probable kinds of genes his animals possess. This, in fact, is the only reason for keeping records.

Other Considerations in Selection of Dairy Cattle.—There are many other considerations to be borne in mind in selecting dairy cattle, only a few of which will be mentioned here.

From a practical standpoint a dairyman desires to have a herd of cows that are not too high-strung and nervous, are easy milkers either at hand or machine milking, and have teats which are neither too large nor too small and are well placed on the udder. He also desires cows that calve easily and without complications and those not particularly subject to going off feed or prone to develop udder troubles, such as leaky teats, mastitis, etc. He hopes to develop a generally vigorous strain of animals and a strain that maintains high production for a long time during each lactation period and remains productive over a long period of years. The matter of longevity is especially important, for it takes about the first 2 years of a cow's productive life to repay the cost of growing her up to two years of age, or her cash cost if purchased. In addition, the range of selection is seriously curtailed if cows stay in the herd but a short time; in other words, the faster the rate of turnover, the less effective can selection be. To evaluate properly all the considerations that have been discussed in this chapter makes it imperative for the breeder to keep records. Many forms have been developed for this purpose, a sample of which is shown in Fig. 183. Most of the characteristics for which or against which we select in dairy cattle are the result of the combined action of heredity and environment. Only with fairly complete recorded data is the breeder enabled to discover the strains and families within his own herd that have a preponderance of the genes which he desires to increase and a minimum of those which he would like to rid himself of.

Finally, the matter of efficiency of feed conversion should receive some attention in making selections. Several investigations have demonstrated that variations in ability to convert feed in excess of maintenance requirements into milk exist among dairy cows. A study by W. T. Smith and one of the authors on the matter of efficiency of feed conversion among 42 cows in the University of Massachusetts Experiment Station herd in 136 lactations over a period of 13 years showed efficiencies ranging from 18.12 per cent to 39.6 per cent, with an average efficiency of 29.25 per cent. One cow put 39.6 lb. of total digestible nutrients into the milk pail for each 100 lb. of total digestible nutrients fed, another only 18.12 lb. In general, the higher producing cows were more efficient. Any cow's rate of efficiency was fairly constant at all ages, being somewhat lower, of course, while the animals were still growing. One bull's

daughters were 5.21 per cent less efficient than their dams, another bull's daughters were 4.17 per cent more efficient than their dams. That efficiency of feed conversion has a hereditary basis seems quite likely. To measure things of this nature requires more feed weighing and record



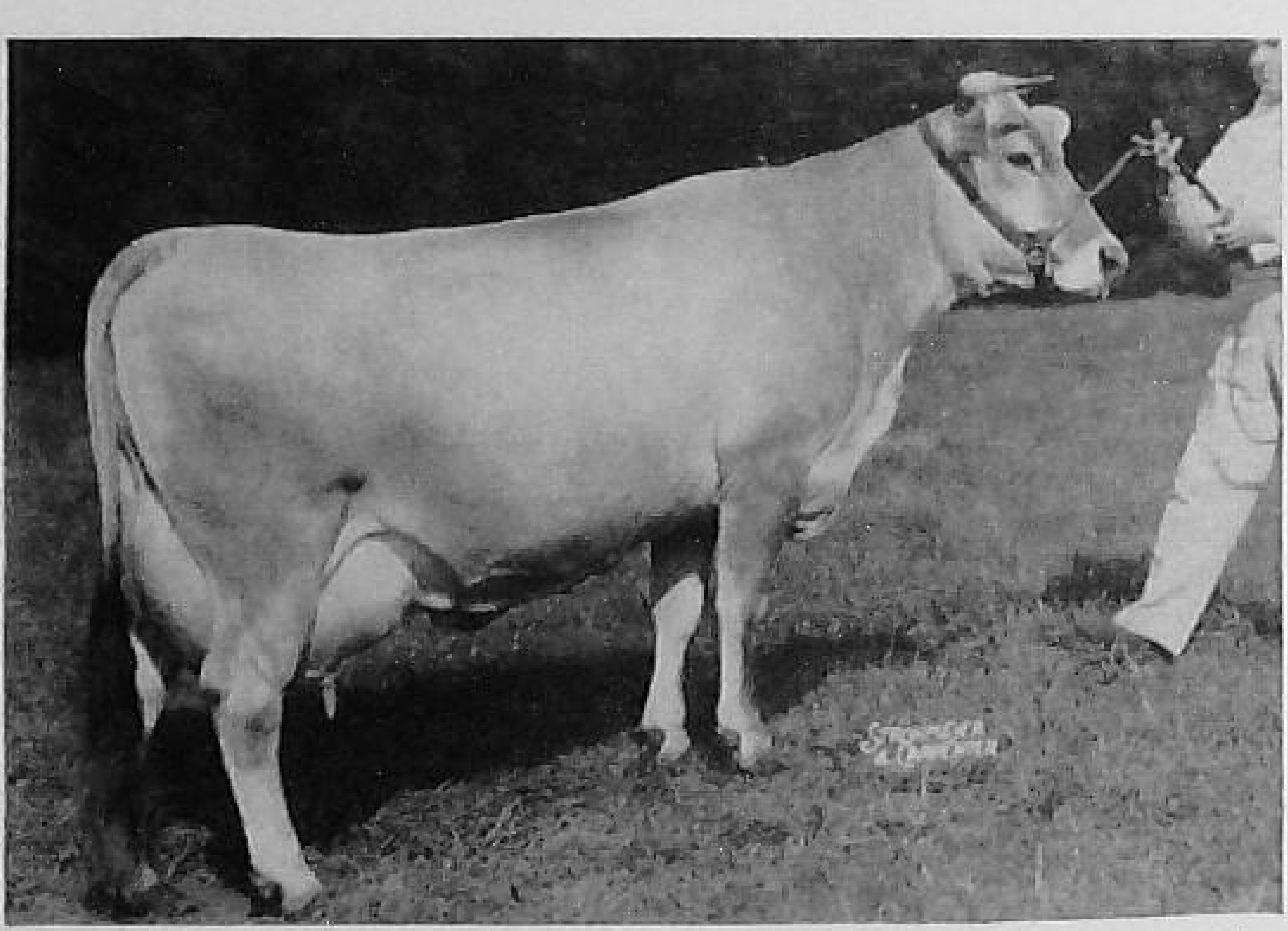


Fig. 187.—Brown Swiss bull (*top*) Bradenhurst Royal Challenger 76657, Grand Champion bull at the 1949 National Brown Swiss Show. He was owned and shown by Charles A. Choate, Old Elm Farm, Winona, Minn.; and cow (*bottom*) Royal's Rapture of Lee's Hill 115541, Grand Champion cow at the 1949 National Brown Swiss Show. Just 2 weeks prior to the show she completed a national champion production record for the breed of 29,095.7 lb. of 4.22 per cent milk, 1228.84 lb. of butterfat in 365 days, 3 times, as a five-year-old. She is owned by Lee's Hill Farm, Morristown, N.J. (*Courtesy of Brown Swiss Cattle Breeders' Association.*)

keeping than the average breeder is equipped to provide, but most breeders can point out cows in their barns that require smaller amounts of high-priced concentrates than do others for the same amount of production. The high correlation between amount of production and effi-

ciency of feed conversion makes it likely that selection aimed at higher production will also to a considerable extent take care of the matter of efficiency of feed conversion.

Only when a breeder knows his own herd average, both as regards anatomy and physiological functioning, is he in a position to tackle the all-important question of selecting his next sire.

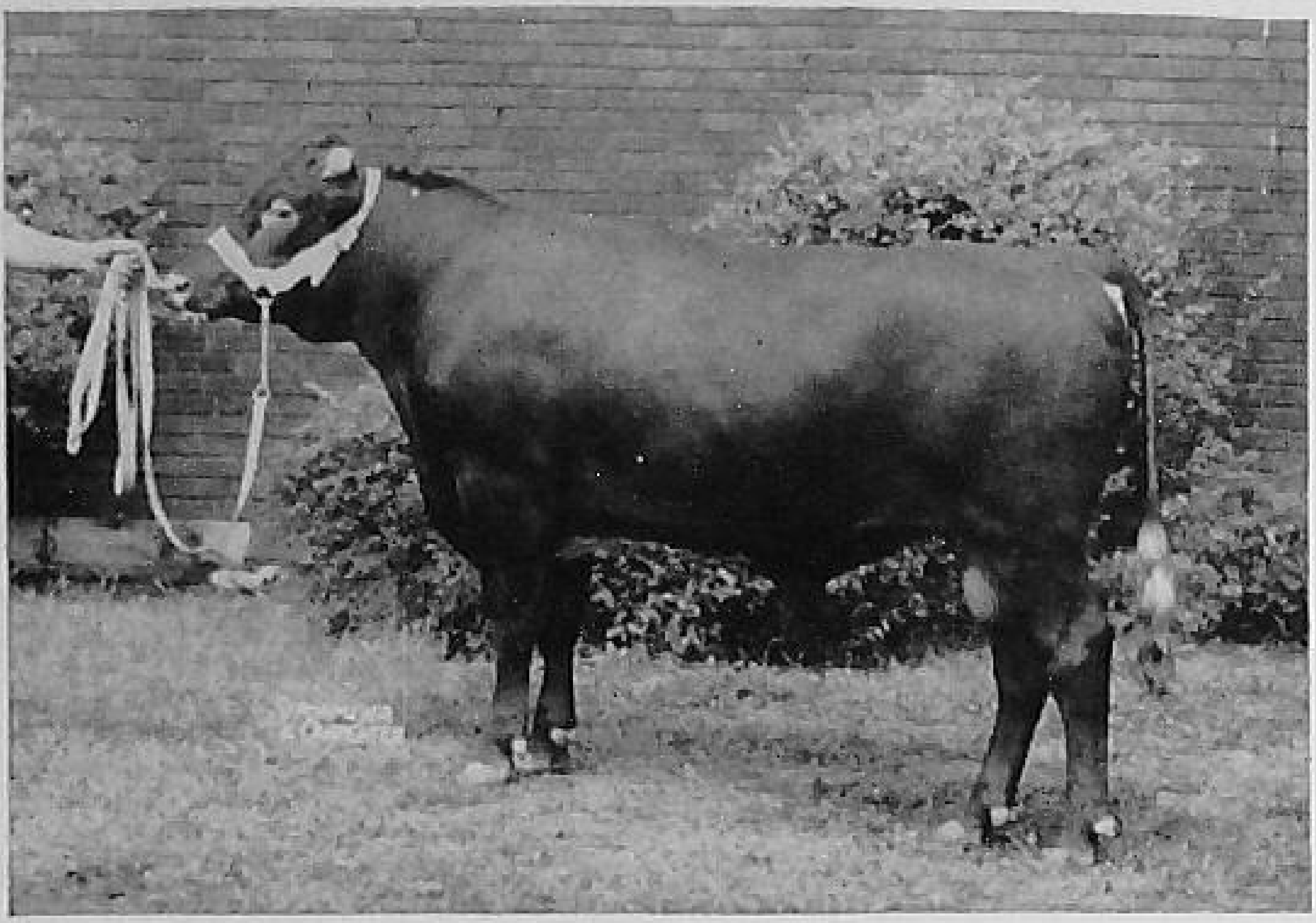
Pedigree Estimates of Dairy Cattle.—The fact that records are quite often available on the females' and daughters' averages or indexes on the bulls in dairy-cattle pedigrees creates a considerable temptation both to investigators and to breeders to try to devise means of apportioning values to the different ancestors and other relatives in order to arrive at a precise genetic value of the pedigreed animal. Sometimes the estimates come very close to the way the animal breeds, sometimes the miss is extensive. Sometimes one way of apportioning value seems best, at other times some other way. If the females' records were never greatly influenced by the environment and the indexes of the males were secured without very great effects from "nicking," from the environment, or from daughter selection, a useful scheme of evaluation might be achieved.

Breeders should study carefully the pedigrees of any animals which they contemplate buying. They should try to ascertain (1) the conditions under which the records were made and (2) how much weeding out of unfavorable material has been indulged in. They should pay particular attention to close-up ancestors and collateral relatives, but relatively little to remote ones. They should include as many close collateral relatives as possible in arriving at their estimate. They should realize that if they can get all the pertinent facts about an animal, they will learn relatively little more by going back further in the direct lines of the pedigree. They should know that only the most favorable data is likely to live in public print. They should be wary of the auctioneer's prattle about animal X being a half brother to a grandson of the Grand Champion at the Whatsis Exposé. They must acknowledge the fact that knowing a pedigree ever so well still leaves one in ignorance of just what genes a sire and dam actually transmitted to an offspring.

As said elsewhere, we like to study the bottom line of a pedigree very thoroughly and demand that those three sires and cows be well-proved animals. If one must arrive at a pedigree estimate by assigning values to ancestors, we believe in doing it on the basis of degree of relationship and without compounding values in direct ancestral lines.

Summary.—It is hoped that the discussions of this chapter have made it evident that the task of selecting dairy animals should be based quite largely on carefully recorded data. Records of production properly standardized can yield an index of a bull's transmitting abilities for

amount of milk and butterfat test. Records on the cows in a breeder's herd can be so arranged as readily to reveal the better female lines in the herd. Records of many other qualities besides production, *e.g.*, health, disposition, type, regularity of breeding, etc., must be available



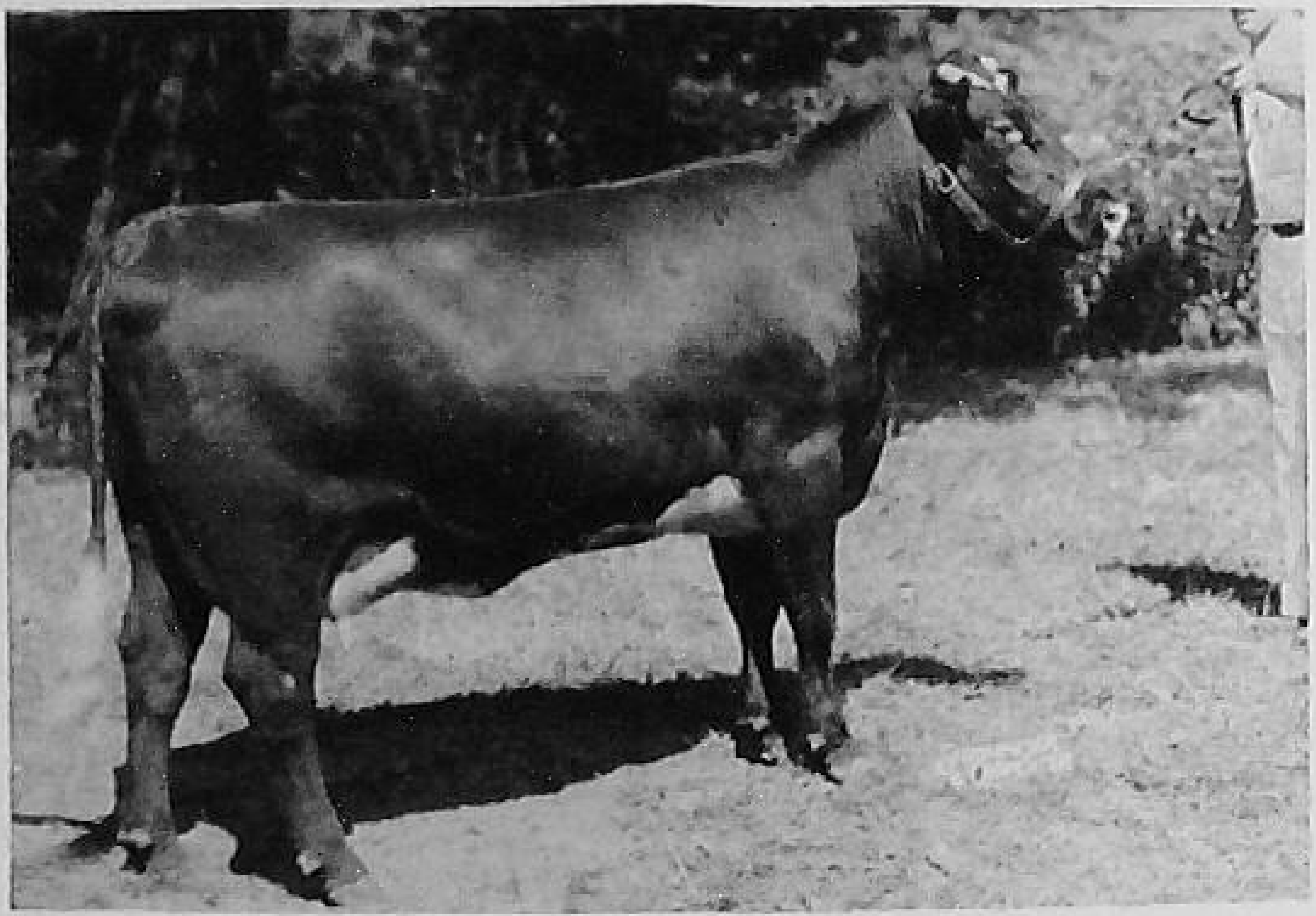


FIG. 188.—Milking Shorthorn bull (*top*) Revelex Daisy's Warrior, Imp. Grand Champion bull at Eastern States Exposition and Michigan State Fair, 1949. Owned by Mystery Farm, Hope, R.I.; and cow (*bottom*) Maidstone Dairy Queen, Grand Champion female at Eastern States Exposition, 1949. Owned by Last Chance Ranch, Lake Placid, N.Y. (*Courtesy of American Milking Shorthorn Society.*)

if a breeder is to be eventually successful in establishing desirable qualities in and eliminating undesirable ones from his herd. When sufficient records are available in a pedigree, it would seem to be possible to predict with considerable accuracy what a projected or newborn individual can be expected to transmit.

Selection in dairy cattle is admittedly complex because many genes are involved, the environment plays such a large role, and we must necessarily select for and against many things simultaneously.

In breeding his own replacements, a man should try to buy bulls whose pedigrees can be filled in with the sort of records that will give some idea as to what the bull in question may transmit to his daughters. If one cannot get a proved bull, he should at least try to get a son of a good proved bull out of a daughter of a good proved bull, and the inclusion of this daughter in a good family should receive at least as much consideration as her own record.

In the purchase of bulls one should avoid those with no tangible evidence of freedom from disease, with sufficient age to be proved but lacking proof, with "holes" in their pedigrees, with a serious lack of the marks of dairy quality, with some good but many poor close relatives, with evidence of weak constitution and general lack of size, with pedigrees too incomplete in terms of proved dairy production.

In the purchase of cows, one should patronize only breeders and dealers of unquestioned integrity and never buy cows with no records of production, with no tangible evidence of freedom from disease, with meaty, pendulous, lumpy, or broken-away udders, with a lack of body capacity and udder capacity, with short necks, chunky, meaty bodies, with narrow pelvis, short, narrow, droopy rumps, with evidence of weak constitution and general lack of size, with a lot of poor close relatives.

In the purchase of heifers, one should avoid those with no tangible evidence of freedom from disease, with no prospect of a sound, large, quality udder, with marked beefy tendency, with a marked deficiency of size for age, with a lack of proved dairy quality in their close relatives, with sire of unknown or poor dairy-transmitting qualities.

The breeder must keep production records on all the females in his herd year after year for the twofold purpose of spotting the "boarder" and of providing himself an opportunity to select wisely in his best cow families.

Our first job as animal breeders is to:

Analyze. Find out what we have. We do this by means of complete record keeping.

and, second, to

Synthesize. Fit together known hereditary materials in our animals into more efficient and more beautiful forms, and we do this by systems of breeding and selection.

Successful dairying depends, in the final analysis, on the inherent milk-producing qualities of the individual cows in the dairy herd. For

efficient, economical production they must be healthy and endowed by nature with the bodily mechanism and temperament that will permit them to consume large quantities of feed and to convert this feed into large quantities of high-quality milk over a long period of years. In order to ensure continuing success for the industry, breeders must contrive ways to create increasingly more efficient animals, and this is only possible through the intelligent application of facts established through honest and unprejudiced record keeping.

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CHAPTER XXII

SELECTION IN MEAT ANIMALS

by

DR. E. J. WARWICK

Basically the task of the breeder of meat animals is to produce animals which will more efficiently convert vegetable products (some edible by man and some not) and inedible waste animal products into nutritious human food products of the quality which will appeal to the human palate. In a world with constantly increasing human population and a consequent narrowing of the margin of safety between world food needs and potential world production, it is essential that this conversion be made as efficiently as possible. From the standpoint of the individual commercial-livestock producer, profit depends upon two things: (1) the cost of production and (2) quality of product as reflected in selling price. Thus, his interests in efficiency are identical with those of the population at large so far as the kind of animals needed is concerned.

In many ways the task of selection in meat animals is simpler than is the case in dairy cattle. The principal favorable factors are: (1) Many characters of economic importance in meat animals are expressed by both sexes; (2) many such characters are expressed before sexual maturity, thus making selection on the basis of individuality possible at much younger ages; and (3) for at least certain characters, *e.g.*, carcass quality, there is a greater correspondence between type of the live animal and true value than there is between type and production in dairy cattle.

Arrayed against these advantages are certain disadvantages which limit progress. Of these the fact that we have no single end point which can be used to measure value is perhaps the most important. As pointed out in an earlier chapter, selection for more than one thing reduces the amount of selection which can be directed toward any one thing. Since meat animals must be selected simultaneously for economy of production and for quality of product and since both of these things depend upon a number of factors some of which may be biologically antagonistic, the difficulty of the meat-animal breeder becomes quickly apparent. Added to these things is the fact that quality of product can best be evaluated only in the carcass and that an animal studied in the carcass cannot be used for breeding!

It cannot be emphasized too strongly that while as an art the breeding of meat animals is old, it is very new as a science. Thus future research work may well change some of our current concepts.

The question of whether we should strive to breed animals which are good in terms of all-around value and then breed them "pure" or "straight" for commercial production or whether it is more feasible to develop certain strains which are superior in one character and then cross them with strains superior in other characters for commercial production is one which must be considered at present as unanswered.

Both procedures have been used in the past, although the philosophy which has largely dominated the thinking of American livestock people has been that of producing desirable purebreds and then using them or

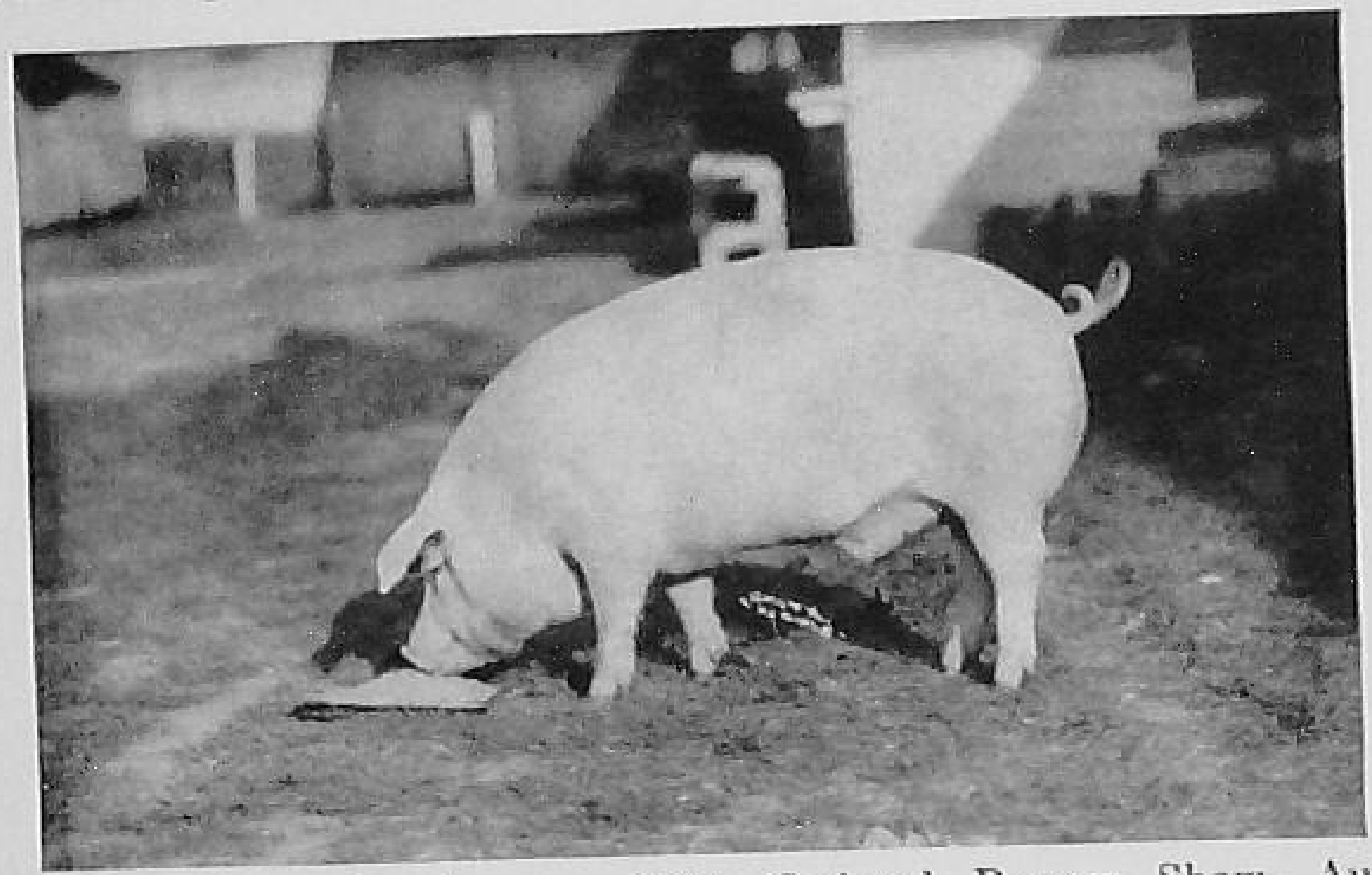


FIG. 189.—Grand Champion barrow, 1948 National Barrow Show, Austin, Minn. Owned and shown by Portage Farms, Woodville, Ohio.

their high grades commercially. Even where crossbreeding has been practiced extensively (as with hogs), crosses have often been made to take advantage of heterosis between breeds which have each been selected along similar lines. The system of using strains which are selected for all-around merit (even if used in crossing) is the most prevalent in the United States. Most of the material in this chapter assumes a breeding system aimed at the production of animals of all-around merit. Some mention will be made of the use of divergent strains for crossing.

The best example of crossing markedly different types in the United States is the system of crossbreeding sheep followed in many range areas in the West. Animals of fine-wool breeding (principally of the Rambouillet breed) possess the vigor, hardihood, and flocking instinct necessary for range-sheep production but lacking in most other breeds. The fine-wool types do, however, lack size and mutton conformation. In an

effort to take advantage of the good qualities of both types, mutton rams are often crossed with fine-wool ewes for the production of market lambs in areas where feed conditions are good enough for the production of fat lambs at weaning. Even under these conditions, efforts are being made to develop pure strains combining as much of the good qualities of both types as possible. The ultimate success or failure of these efforts will, to a large extent, determine whether the current crossbreeding practice is a transitory stage or a permanent part of the sheep industry of the area.

In Great Britain considerable stress has been placed upon the development of strains adapted to particular areas. These adapted strains are used to furnish the basic stocks for commercial production, but are used in various crossbred combinations. As an example of this scheme, consider the place of the Blackfaced breed of sheep used on the rugged hill land of Scotland. This breed is noted for exceptional vigor and the ability to survive and reproduce under adverse conditions. However, even when the environment is favorable and optimum nutrition is provided, carcass quality is still mediocre. When ewes of this breed are mated with mutton-type rams, such as the Border Leicester, the resulting lambs, if properly fed, yield satisfactory carcasses. The male offspring of this cross are sold for mutton while the females are taken to good pastureland and bred to mutton-type rams of the Down breeds, with all the offspring going for slaughter.

Systems of sheep breeding similar to this also exist in Australia and New Zealand. Nichols[1] has termed this "stratification" of an industry and has pointed out that it may occur in time as well as space.

Type as the Basis for Selection in Meat Animals.—Legend tells us that Bakewell gave attention to economy of production in his breeding operations and various animal husbandry writers have stated that the master breeders of the past insisted upon high and economical production of meat before animals found favor with them. It is, of course, impossible to check on the accuracy of such statements. In view of the fact that satisfactory objective measurements of such things were lacking, it appears more probable, however, that most selection during the pioneer stages of livestock improvement was based on visual appraisals of body form or type, just as has been the case up to the present time.

To a certain extent type is production in meat animals, being related especially to quality of carcass. The ability of trained judges to predict carcass grades from an examination of the live animal just prior to slaughter is quite high if a considerable range of variation is present. The ability to predict small differences in carcass grades or scores of

[1] See Nichols, 1945, for summary and reference to earlier papers.

animals of uniform type from visual appraisal of the live animals is much more limited. This is illustrated by figures calculated from the work of Semple and Dvorachek (1930). Eight lots of slaughter cattle totaling 66 head, including two lots of purebred Angus, two lots of "native" animals, two of first crosses, and two of second crosses, were graded on foot just before slaughter. The total correlation between live-animal grades and carcass grades was +0.87, but within lot the correlation was only +0.50. Apparently the judges were able to differentiate quite successfully between types but were less able to predict carcass quality of more or less uniform animals.

The frequent disagreement of placing between "on foot" classes and the carcasses of the same animals in livestock shows where such classes are included is another illustration of the difficulty involved in predicting differences in carcass quality among animals all of which are presumably fairly satisfactory or they would not have been entered.

Perhaps the point is that after the essential factors in good meat type are attained, visual evaluation is largely based upon details of conformation which actually are of little or no importance in determining carcass quality.

However, the broad agreement between type and carcass quality makes it imperative that the meat-animal breeder strive to have the essentials of good type in his herd.

Without attempting to enumerate the various points to be observed in evaluating the type of meat animals of the various classes, it can be stated in general terms what constitutes good meat type. Anatomically, the desirable meat-type animal is low-set, blocky, and compact. Maximum development of the loin and rear quarters and maximum muscling of the rib is sought, since these regions have the greatest market value. In the finished animal, smoothness and evenness of contour, mellowness and firmness of fleshing, proper degree of fat covering, and indications of quality in hair, skin, and bone are qualities sought by breeders, even though they may not be related to carcass quality.

Hammond,[1] together with several of his coworkers, has developed the idea that animals change in body proportions with advancing age, the young animal being largely head and legs but gradually lengthening and deepening with age so that the proportions of the more valuable parts, such as the loin and rear quarters, are increased in relation to the less valuable parts, such as the head, neck, and shanks. In general, the tissues tend to develop in the order: skeleton, muscle, and fat, but with additional growth gradients running from the cranium backward and from the tail forward meeting in the region of the loin. Thus, for

[1] See Hammond, 1940, for discussion and references to earlier papers.

example, fat is the slowest tissue to develop in an animal, and the loin region is the last to fatten.

Hammond believes that the principal change brought about by selection for improved meat type is to speed up these changes so that they

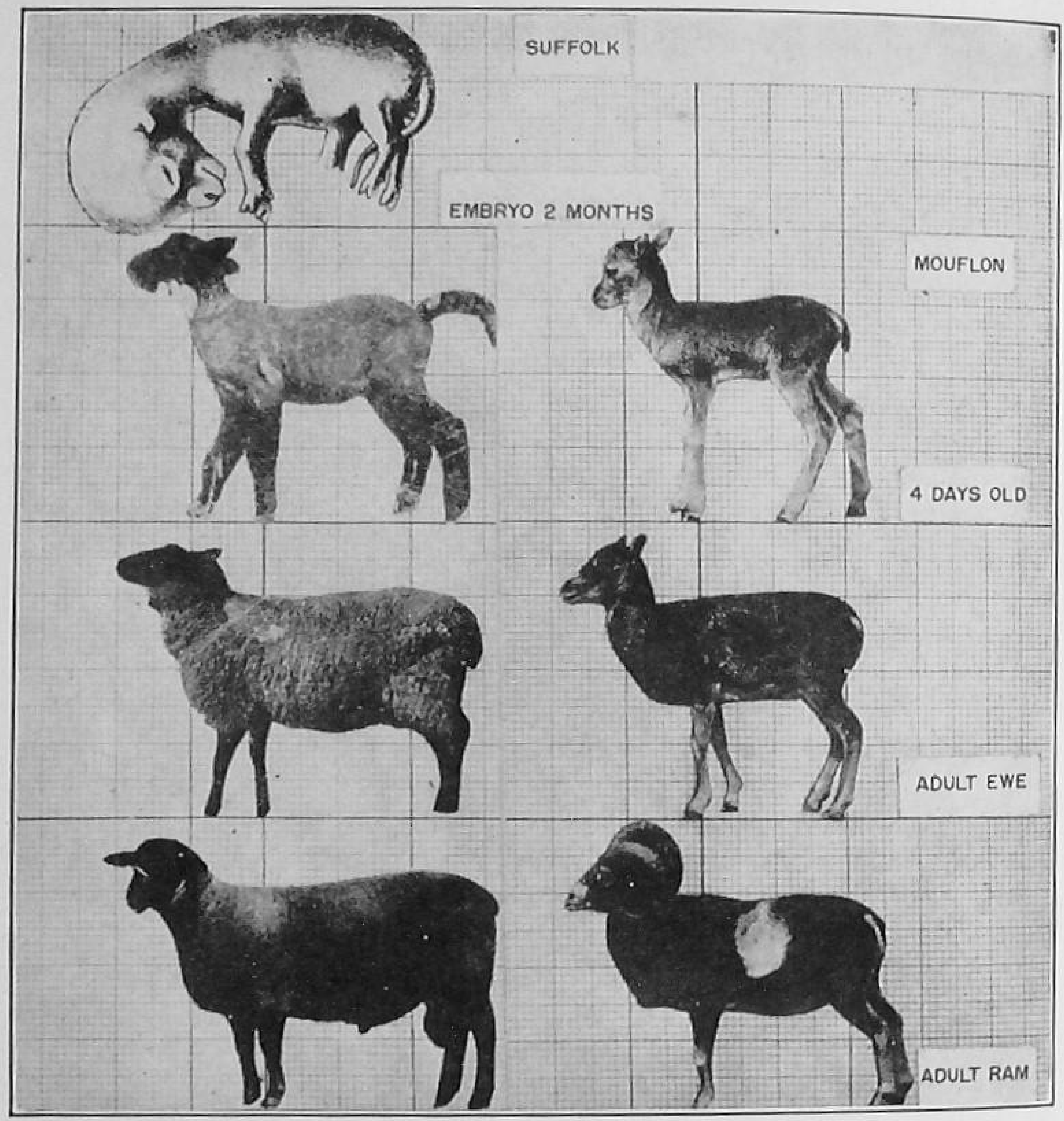


FIG. 190.—Changes in body proportions of sheep with advancing age. The Suffolk, an improved mutton breed, is compared with an unimproved breed, the Mouflon. *(Courtesy of Dr. John Hammond, Cambridge University, Cambridge, England.)*

occur at earlier ages and continue to a greater degree. This process is illustrated for sheep in the accompanying figure.

Obviously, the speed with which these changes take place depends upon both the genetic make-up of the animal and the plane of nutrition upon which it is kept. Animals have been developed which, under good nutritional conditions, are finished at lighter live weights than are

economical for the producer and lighter carcass weights than are desired by the consumer. Thus, correct meat type can be defined as the type permitting maximum development of the high-priced cuts and optimum finish under the nutritive conditions which will prevail in a particular type of production and at carcass weights in demand by the consumer. Since climatic and feed conditions vary from area to area, and since there is variation in consumer demand, it is obvious that the same type of animal, so far as rate of maturity is concerned, may not fit all conditions.

Correlations between type and the factors influencing economy of production seem to be of a much lower order than those between type and carcass quality. Thus, the best procedure in evaluating animals for these characters seems to be the use of production records. In spite of the generally low correlations between type and productivity, a few items are apparently highly enough related to productivity to make their consideration by breeders worth while.

Type in swine has long been thought to be related to prolificacy, and the work of Zeller and Hetzer (1944) provides experimental evidence on the point. Herds of small-, intermediate-, and large-type Poland China hogs were studied. The intermediate- and large-type sows weaned litters averaging about one pig larger than those of small-type sows. The intermediate and large pigs were heavier at birth and at weaning, and grew somewhat faster after weaning. Earlier work at the Illinois Station (Carroll *et al.*, 1929) in which groups of weanling pigs of types ranging from very chuffy to very rangy were fed out, indicated that type was not a controlling factor in rate of gain, although there was a suggestion that the very chuffy types gained somewhat more slowly than the other types.

These experiments seem to indicate that if maximum prolificacy and growth rate are to be obtained in swine, a type with at least reasonable length of body must be bred.

Aside from a low relationship between size and rate of gain in beef cattle and sheep, most studies have shown little relationship between visual body-type characters and characters of productive importance.

The greatest danger in basing selections exclusively upon visual-type appraisals rather than production records is that "fads" having no relationship, or perhaps even a negative relationship, with true productivity may come to be the dominant factor in selection.

The dangers from such practices can be best illustrated by two examples in sheep. It was long assumed that sheep with wrinkled skin should have more area upon which to grow wool and would therefore produce heavier fleeces than smooth-bodied types. Another apparently equally logical assumption was that a covering of wool extending well down

over the face should be indicative of a strong wool-growing tendency and therefore indicative of fleece production. These two assumptions served as the basis upon which several breeds of fine-wool sheep were selected for an extremely wrinkled condition and upon which both certain fine-wool and medium-wool breeds were selected for an extensive face covering —extending in extreme cases clear to the muzzle.

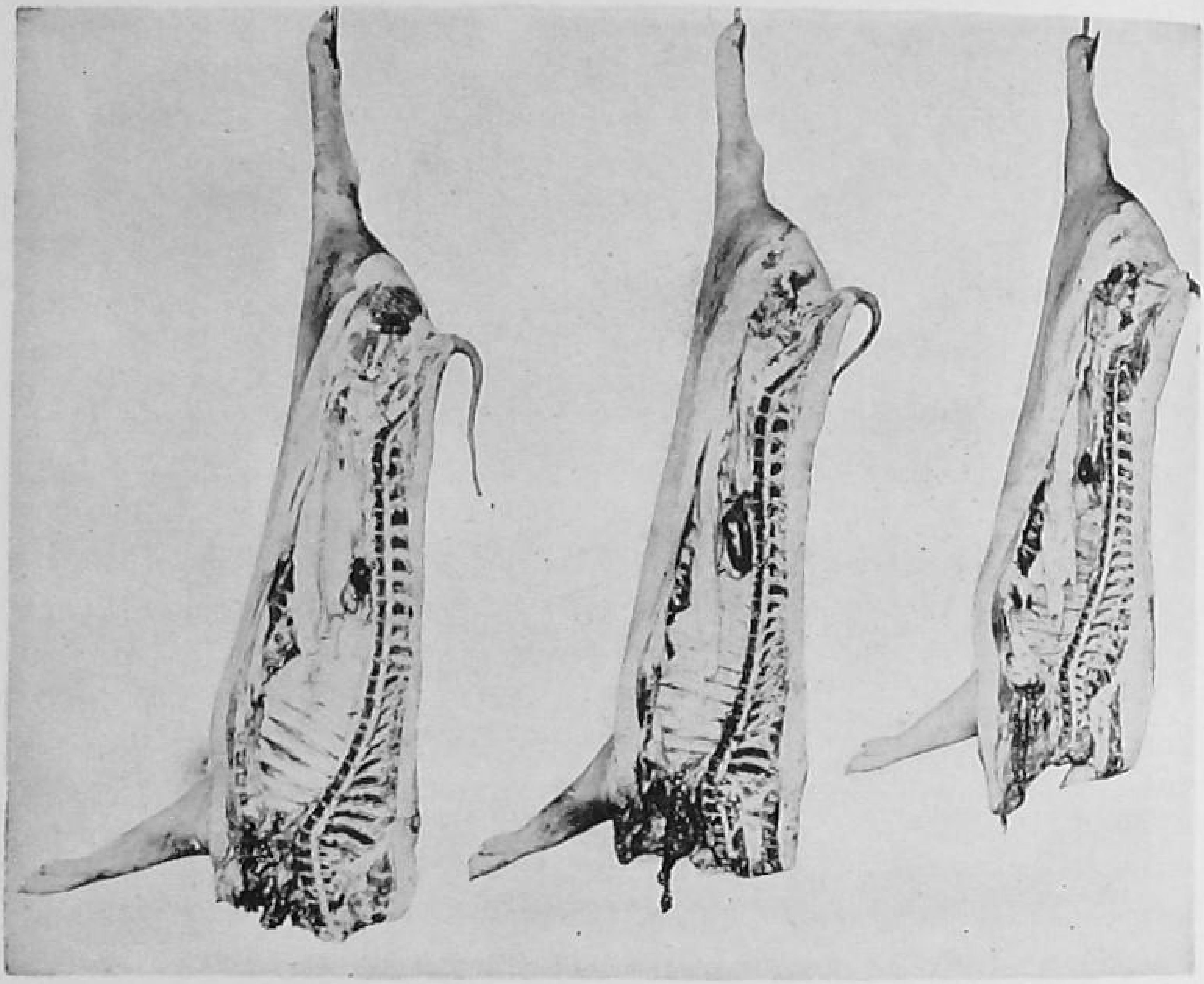


FIG. 191.—Dressed carcasses of large-, intermediate-, and small-type hogs, slaughtered at approximately 225 lb. in weight. (*From O. G. Hankins, A Study of Carcass Characteristics in Relation to Type of Hog, Amer. Soc. Anim. Prod. Proc.*, 1940.)

Systematic studies over a period of years especially by the U.S. Department of Agriculture (Spencer and Hardy, 1928) and the Texas Agricultural Experiment Station (Jones *et al.*, 1944) have shown that the wrinkly types do produce more pounds of grease wool than the smooth types. The differences practically disappear in scouring, however, so that the weight of clean wool produced by the two types is almost equal. In addition, the staple length was longer in the smooth types, and fiber diameter was more uniform. Observation indicates that the smooth types are easier to shear and less susceptible to fly-strike. Thus, the evidence seems to be clear that the wrinkly types do not have the wool-

producing superiority claimed for them and that they are undesirable in other respects.

Extensive studies have likewise shown that extreme face covering is undesirable. Probably the deficient production is dependent upon the

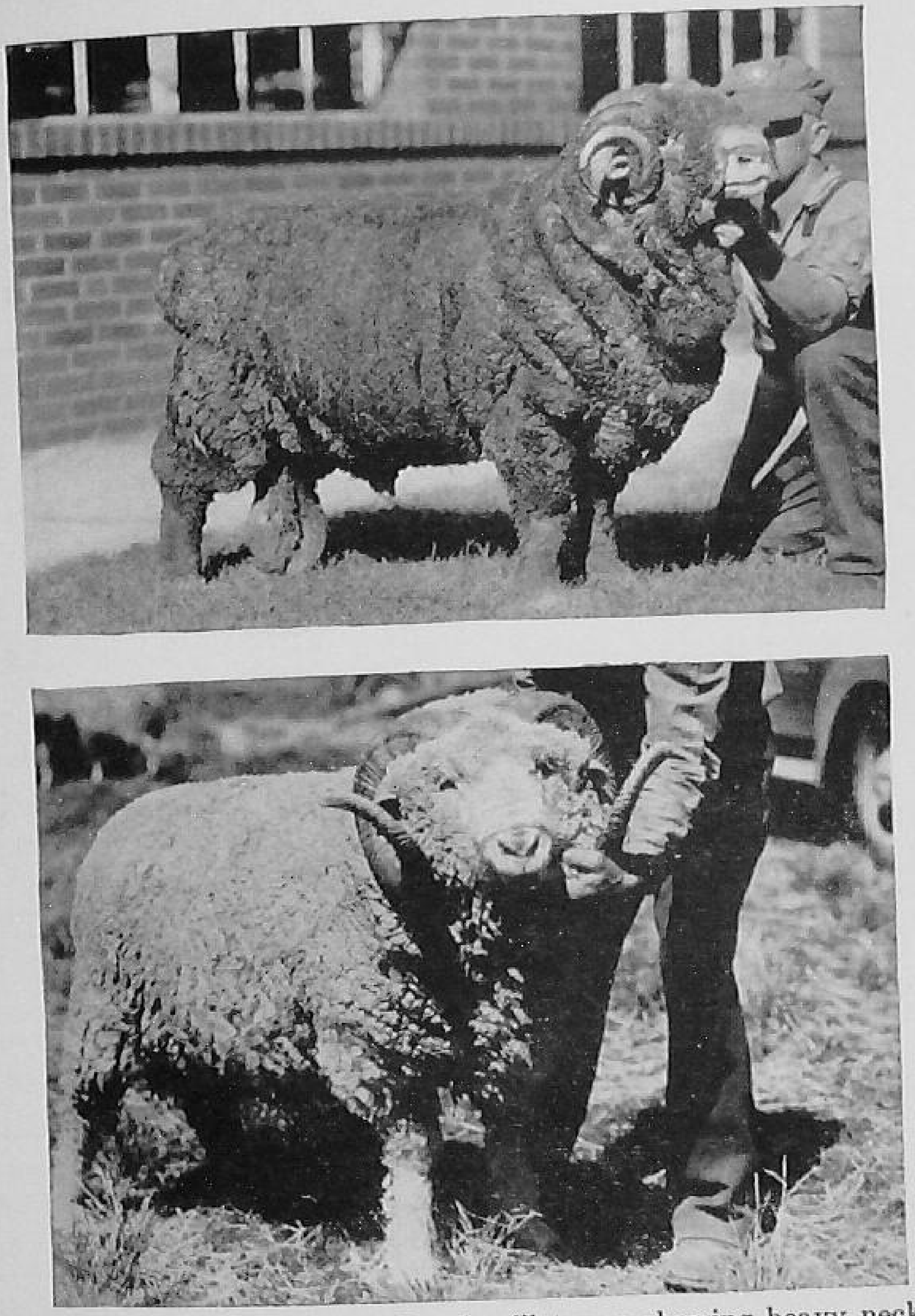


FIG. 192.—*Above*, a champion B type Rambouillet ram showing heavy neck folds and a moderate degree of wrinkling on the body. *Below*, a range Rambouillet ram almost free from wrinkles. Note the difference in degree of face covering in these two rams. (*Courtesy of Bureau of Animal Industry, U.S. Department of Agriculture.*)

excessive growth of wool covering the eyes and causing "wool-blindness" which interferes with the ability of the animal to feed properly. Figures in Table 51 taken from a recent report of Terrill (1949) indicate that under range conditions Rambouillet ewes with covered faces are seriously deficient in lamb production. The last column in the table, indicating

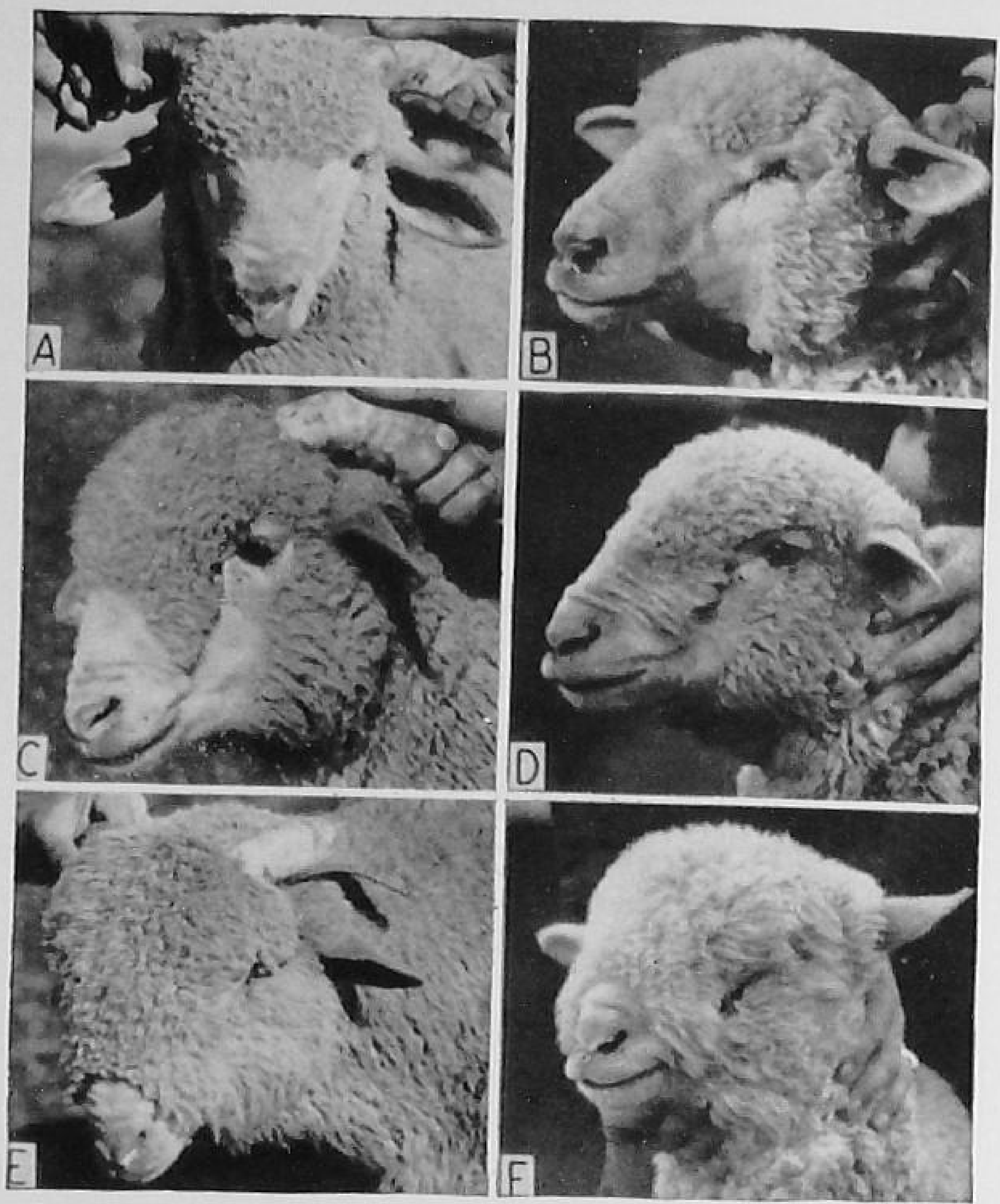


FIG. 193.—Variation in degree of face covering in sheep. The animals shown in *E* and *F* are definitely "wool blind." (*Courtesy of Western Sheep Breeding Laboratory, Dubois, Idaho.*)

a difference of 11.1 lb. in lamb produced per ewe bred, is especially striking.

TABLE 51.—RELATION OF FACE COVERING TO LAMB PRODUCTION

Face covering	No. of ewe years	% ewes lambing of ewes bred	% lambs born of ewes lambing	% live lambs of lambs born	% lambs weaned of live lambs born	Av. weaning weight, lb.	% lambs weaned per ewe bred	Pounds of lamb weaned per ewe bred
Open....	286	95.5	126.7	91.9	89.0	76.3	99.0	75.5
Partially covered	845	95.4	124.2	92.3	88.1	74.8	96.3	72.1
Covered.	1,557	91.9	119.7	90.0	88.6	73.4	87.7	64.4

Not only were the covered-face ewes inferior in lamb production, but were not importantly superior in wool characters. A few statements from Terrill's paper[1] give a concise summary of the work:

Ewes with open faces produced 11.3 percent more lambs and 11.1 more pounds of lamb per ewe bred than those with covered faces. Ewes with partially covered faces weaned 8.6 percent more lambs and 7.7 more pounds of lamb per ewe bred than those with covered faces. Differences in face covering within these groups were associated with corresponding differences in lamb production. These advantages for ewes with open faces occurred in spite of three periodic clippings around the eyes of all ewes subject to wool blindness.

About 46 percent of the advantage of open-faced ewes was due to a greater number of lambs born per ewe lambing; 26 percent was due to higher weaning weights; 19 percent was attributed to a higher proportion of the ewes becoming pregnant; and 9 percent was due to greater viability to weaning of offspring.

Open-faced ewes excelled covered-faced ewes in lamb production at each year of age. The greatest advantage for open-faced ewes in pounds of lamb per ewe bred was found at 3 years of age followed in order by 2, 4, 6, and 5 years.

The yearling grease and clean fleece weights and staple lengths of 2,499 Rambouillet ewes and the lifetime grease fleece weights of 798 Rambouillet ewes were slightly greater for covered-faced ewes than for those with open faces. The differences were not significant except for staple length and were not large enough to be economically important.

The great economic importance and high heritability of face covering indicate that it should receive as much or more attention in selection than any other trait in sheep if wool blindness is a problem.

The moral to be drawn from such studies is obvious, namely, that present-day breeders should critically examine existing breed standards and, if necessary, research should be carried out to determine whether they are compatible with the production of the most efficient and profitable animals. Obviously, such critical tests should be applied to fads which are certain to be started in the future *before* and not *after* they have become so widespread as to seriously handicap the usefulness of a breed.

Evidence that responsible leaders among breeders are aware of the necessity of this approach comes from the fact that the American Hereford Breeders' Association is currently (1950) sponsoring research in cooperation with four state experiment stations on the question of type in that breed. The need for such work arose from the facts that (1) over a long period of years, show rings have tended to favor an increasingly thick, compact, early maturing type of animal which seemingly has been accompanied by some loss of size and ruggedness, and (2) during recent years an ultracompact type known as "comprest" has arisen in the breed

[1] *Jour. Anim. Sci.*, August, 1949, pp. 360–361.

and has found favor in some livestock exhibitions. Objective evidence on the relative value of these various types for commercial beef production is lacking, and the officers of the association are to be commended for their research approach to the question.

Research on the problems at the Colorado Station has to date shown the following trends:[1]

1. There were no consistent or great differences in pounds of feed required to make a pound of gain in steer calves of conventional or small types. Small-type steers gained less per day and consumed less feed per day. Rate of gain and efficiency were not associated between these groups.
2. Small-type steers when killed at the same degree of fatness as conventional-type steers weighed about 150 pounds less than the larger type.
3. The percentages of carcasses in the different wholesale cuts were almost identical for the two types of steers. The carcasses of the small steers weighed 402 pounds, those of conventional type weighed 500 pounds at the same slaughter grade.
4. Cows of large, intermediate, and small types have eaten amounts of hay during the winter almost directly proportional to their body weights. Heifers, full fed, consumed hay relative to body weight, but required considerably more hay per unit of body weight than did cows.

The work as being carried out at the other three stations includes steers of small, medium, and large types with representatives of each type being fed out under three different regimes, namely (1) fattening by full feeding as calves, (2) grazing as yearlings followed by a dry-lot fattening period, and (3) fattening on grass as two-year-olds. Quite possibly the same type of steer will not prove to be best under all three types of management.

The position an individual breeder should take if some fad he knows to be uneconomic should sweep his breed is a question for thought. Should he follow the fad in order to produce animals for which there is an immediate market or should he make the financial sacrifice of staying with an *unpopular* but basically *better* type? That this is not a hypothetical situation is illustrated by the story of Peter Mouw of Orange City, Iowa.

During the period around 1900, and particularly during the few years immediately following the turn of the century, the Poland-China breed of hogs was swept by the so-called "hot-blood" craze in which selection was for an extremely small, short-legged, refined, early maturing type of hog. Mr. Mouw and a few other breeders believed this to be a basically unsound type of hog and continued to produce a more rugged

[1] Beef Breeding Research in Colorado, Progress Report, Colorado Agr. Exp. Sta., July 6, 1950 (mimeo).

"big type," which was often the subject of ridicule at the shows. The tide finally turned, however, and overnight these hogs became the most popular in the breed. Adherence to an ideal paid off with a small fortune to Mr. Mouw in this case.

Many breed trade-marks are neither positively nor negatively correlated with productivity but are nevertheless a problem for breeders. The amount and distribution of white in breeds with white color markings apparently is very low in heritability. Genetic knowledge at present indicates that rigid adherence to a set color pattern is difficult, if not impossible, to fix. Therefore, if the breed requires certain markings, a portion of young animals will be ineligible for registry regardless of their excellence in other regards. Discarding these animals automatically lowers the amount of selection which can be practiced for more important characters and cannot help being a drag on the progress of the breed. A statement several years ago by the late E. M. Harsch, secretary of the Hampshire Swine Registry Association, in which he said that "a few white hairs on the hind legs or a black spot the size of a dime in the belt is truly a long ways from a pig's heart" seems to express a common-sense attitude toward minor deviations from a set color pattern.

To summarize our discussion of type, it can be said that the breeder should endeavor to select for the fundamentals of good meat type—items known to be positively correlated with true worth and regarding which our ideals are not likely to change greatly within the forseeable future. On the other hand it is imperative that he not espouse a new fad until it has been shown to be clearly superior to existing types. He should avoid placing undue emphasis on "frills" or "fancy points," even if they are in themselves harmless.

Use of Production Records as a Basis for Selection in Meat Animals.—Since meat animals are kept for profit, it would seem axiomatic that selection should be directed principally toward those things which have a direct influence on productivity (in the broad sense) and thus on profitability. If type were perfectly correlated with productivity, it could logically serve as the sole basis for selection. Since, as we have seen, this correlation is at best of a low order, a priori reasoning indicates that selection could be better if based on actual production records themselves. Selection for type will then be automatic in so far as it is correlated with productivity.

The ease of measuring speed, milk production, and egg production, in racehorses, dairy cows, and laying hens, respectively, led to the use of production or performance records in selecting breeding animals in these classes of stock long before such records were used for meat animals.

The problem of using production records in meat animals is more

difficult than in the classes of stock just mentioned because no one measurement accurately evaluates the worth of an animal. Extensive studies have been made of the factors which should be considered in breeding meat animals, however, and today we have a fairly clear idea of the things which should be considered, although the exact importance which should be given to each factor is not known. It probably varies under different conditions. For example, in producing for a discriminating market, quality of product may be the most important factor influencing profitability. On the other hand, in producing for a market which does not pay for quality, economy of production is the most important.

Specific record-of-performance procedures for each class of livestock have been developed which should serve as the basis for selection, regardless of whether selection is based on individuality, pedigree, or progeny test. The use and limitations of such procedures will be discussed in later sections on each class of animal.

Certain general procedures must be followed if production records are to be kept and used for selecting breeding animals. Accurate pedigree records must be kept, and each individual animal must be positively identified by means of ear notches, ear tags, brands, or tattoos. Accurate records of birth dates must be kept, and weight records must be taken at certain specified ages. In so far as possible all young animals should be raised under similar conditions of care and management, since records of relative growth rate would be worthless from a genetic standpoint if animals had been fed differently. Animals should be kept under practical conditions, since records made under forced conditions (such as with nurse cows) may have little relationship to true value under normal conditions.

Thus, it can be seen that the keeping of production records represents an expenditure of time and labor—an expenditure which is highly worth while, however.

The exact record forms to be used will depend upon the person using them. Some forms which have been found satisfactory are given later in this chapter. They will serve as a source of ideas for the person who desires to design his own records.

Although production testing may be worth while as an aid in culling the female side of a herd or flock, it loses most of its effectiveness if sires without production records are continually introduced into the herd.

Thus, most of the discussion in the remainder of this chapter assumes either (1) a closed herd with home-produced sires being used or (2) the purchase of sires from production-tested herds. In the latter case a purchaser should study the environment of the herd where sires are

produced in relation to that of his own herd to be sure the production records do not depend upon skillful management alone.

Relation of Environment to Selection in Meat Animals.—It has long been recognized that animals of improved meat types tend to resemble unimproved types when raised under suboptimal nutritional conditions—hence the origin of the old saying that "half the breeding goes in the mouth." Moulton *et al.* (1921 and 1922) showed that in cattle the major tissues, bone, lean, and fat, were differentially affected by a low plane of nutrition, with bone growth being affected the least and fat deposition the most. Several other workers have confirmed this basic tendency in other species of farm animals.

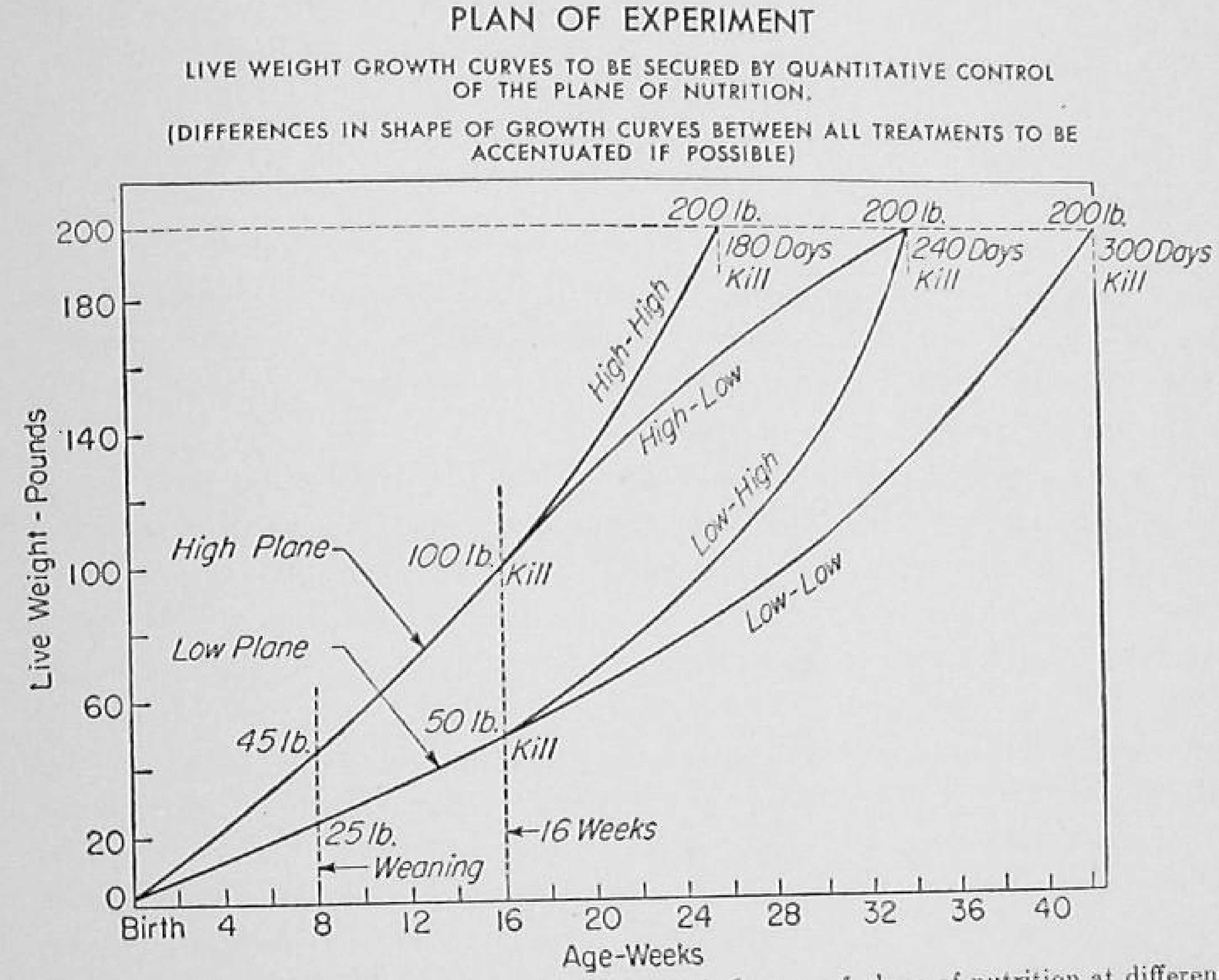


FIG. 194.—Plan of experiment to determine the influence of plane of nutrition at different periods with respect to age upon growth rate and carcass composition in bacon hogs. (*Courtesy of Dr. C. P. McMeekan and Dr. John Hammond, Cambridge University, Cambridge, England.*)

McMeekan (1940–1941) made a detailed study of the growth and carcass composition of pigs of an inbred Yorkshire strain when fed from birth to a slaughter weight of 200 lb. on various feeding regimes. Pigs were divided at birth into two groups, with one fed on a high plane and the other on a low plane for the first 16 weeks of life. At that time half the pigs on each plane of nutrition were shifted to the other so that four

nutritional regimes resulted, namely, groups fed on (1) a high plane from birth to slaughter (high-high), (2) a high plane from birth to 16 weeks and a low plane from that time to slaughter (high-low), (3) a low plane from birth to 16 weeks and a high plane thereafter (low-high), and (4) a low plane from birth to slaughter (low-low).

It was found in this work that if the pig is grown so slowly as to be stunted early in life, the early growing parts of the carcass, such as head, legs, and bone and to a lesser extent muscle, are permanently reduced in size. When these animals are later put on a high plane of nutrition, the later developing parts, particularly fat, grow rapidly and result in a carcass too fat for bacon. Conversely, pigs fed from birth on a high plane have a rapid development of the early growing parts and

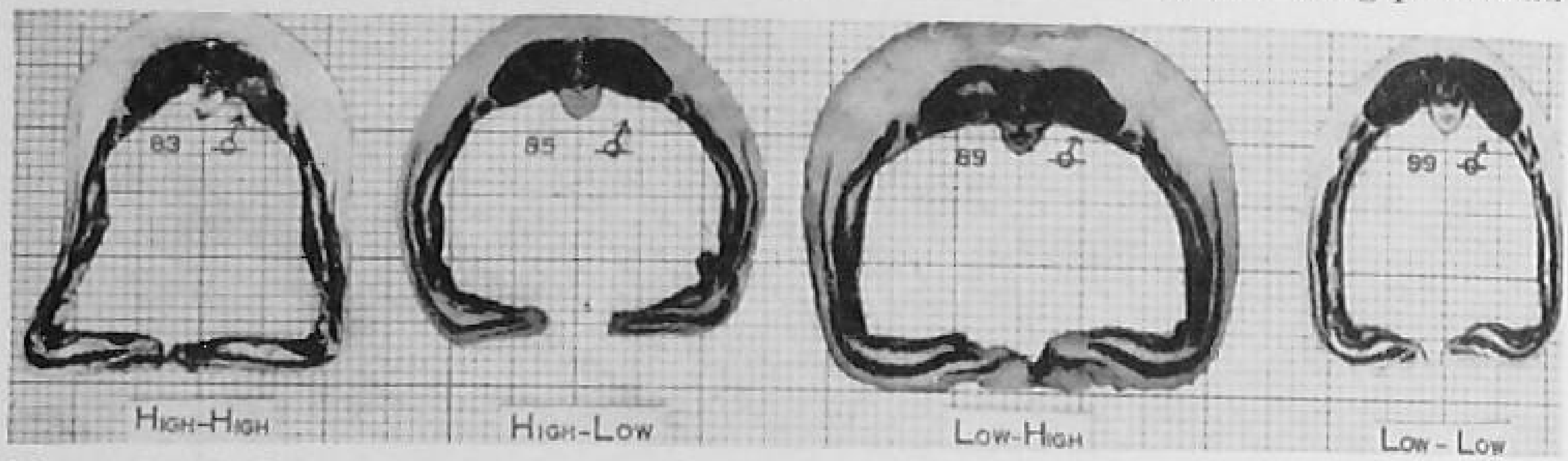


FIG. 195.—Influence of plane of nutrition upon carcass composition of bacon pigs as illustrated by cross sections at the last rib. Pig 83, killed at 168 days of age, maintained on high plane of nutrition throughout life. Pig 85, killed at 196 days of age, was changed to a low plane of nutrition at 16 weeks. Pig 89, also killed at 196 days, grown on a low plane of nutrition the first 16 weeks. Pig 99 was maintained on a low plane of nutrition throughout and required 315 days to reach the standard slaughter weight of 200 lb. (*Courtesy of Dr. C. P. McMeekan and Dr. John Hammond, Cambridge University, Cambridge, England.*)

if later put on a low plane of nutrition produce carcasses with a high content of lean. In a similar experiment with sheep Verges (1939) showed that carcass composition may be materially altered by controlling the shape of the growth curve.

These experiments and others which could be quoted point definitely to the fact that environment exerts a control over development. The animal breeder is vitally interested in the questions of (1) how to properly evaluate known differences in environment so far as their effects on potential breeding stock are concerned, and (2) what type of environment should be used in breeding foundation stocks for ultimate commercial use.

The old saying, that "fat is a good color," shows that the first of these problems has long been recognized. From the standpoint of the sales value of an animal it often happens that putting on a degree of finish far and above what the animal needs for proper development will improve the appearance (apparent type) enough to be a profitable investment for the seller. This is apparently the principal reason for the high and often

excessive degrees of finish so often seen on meat animals in our shows and sales rings.

The question the practical breeder, interested in true improvement more than immediate sales value or show-ring glory, has to answer is how he can logically make allowance for differences in environments to which various animals have been subjected during growth. There appears to be no absolute rule which can be laid down, but certainly the growth rate and apparent type of an animal should be discounted somewhat if it is known to have been forced unduly. Conversely, an animal reared under poorer-than-average conditions should be given some credit over and above what its record and appearance would entitle it to. In some cases, such as the difference in growth between twin and single lambs, it is possible to determine the average effect of a certain environmental factor and make suitable adjustment for it.

The question of what environment a breeder should provide for his animals is a broad question for which no one answer can be given. It has sometimes been assumed that animals should be bred in the best environment possible and that the commercial producer who will use the animals produced should strive to bring the environmental conditions under which he raises his stock up to the same level.

This viewpoint is unrealistic because there are vast areas, such as range country, subtropical areas, etc., where environmental conditions can in all probability never be made ideal but which can if properly used support large numbers of meat animals and add tremendously to our meat and wool supplies. The same argument applies to the utilization of much feed that would otherwise be waste in areas where more intensive agriculture prevails.

The prevailing opinion among animal-breeding specialists in the United States seems to be that animals should be bred and selections made under the same environmental conditions where their descendants will be used commercially. This general plan would seem to have much to commend it since adaptation to the environment at hand is the first essential for successful production.

The folly of departing far from this plan can be illustrated by the general low productivity of our common breeds of beef cattle when placed under tropical or subtropical conditions where their thermoregulatory mechanisms are inadequate for keeping body temperatures down. The development of these breeds in temperate climates has not fitted them for use in hotter areas.

At the present time there is a considerable amount of effort being put into the development of strains of beef cattle suitable for use in the southern regions of the United States and containing various percentages

of the blood of Zebu or Africander cattle which carry more genes for heat and insect resistance than are present in our beef breeds. The best known of these is the Santa Gertrudis (Rhoade, 1949) which is already an established breed. It would seem axiomatic that development of these types should continue in that region, even though regions with better feed conditions might be found.

Hammond (1940, 1947) has developed a point of view which differs somewhat from that outlined above. He feels that, if the environment is so poor as to put a virtual ceiling on development, there will be little chance for inherent differences in gaining ability, type, or production to be expressed and that under such conditions there is little or no chance for a selection program to be effective. He therefore recommends that if we are attempting to make improvement in a given character we should place the animals in an environment which will develop that character to the utmost and then make selections from among those which show it to the greatest degree, even if the descendants are later to be used under poorer conditions.

No experimental evidence is available to indicate which of these rather divergent viewpoints is correct. The most common procedure to date in the United States seems to have been more in line with Hammond's viewpoint. Our purebred herds and flocks have for the most part been maintained in areas where feed conditions are good and other environmental conditions not extreme. Animals from these herds have then provided foundation stock for commercial production in all areas of the country. This situation, together with the nation-wide promotional activities of many of our breed associations, has sometimes tended to result in animals of the same general types and breeds being raised in virtually all parts of the country regardless of their adaptation.

Since meat animals are often maintained in this country under range conditions or other types of environment which may not be adequate in many cases to produce animals with enough finish to meet market demands, it is common to use such areas as breeding grounds, and to move the potential market animals into an area where better feeding conditions prevail for a fattening period before marketing. Such animals must thus have the abilities to (1) survive and grow under suboptimal conditions and (2) fatten readily and produce desirable carcasses when given the opportunity.

Therefore, the logical system to use in producing sires for use in range herds and flocks would seem to be to maintain the purebred breeding herd under typical range conditions and raise the potential sires to weaning there. A preliminary culling could be made at weaning, eliminating those which are undersized or otherwise undesirable. The

remaining animals could be put on feed and further culling done on the basis of rate and efficiency of gain and apparent body type after a feeding period.

Selection in Swine.—From a breeding standpoint the following items are of primary importance in determining the efficiency and profitability of swine:

1. Litter size.
2. Weight per pig and per litter at weaning time.
3. Daily gains between weaning and marketing.
4. Efficiency of feed utilization.
5. Body type or carcass desirability.

Although greatly influenced by herdsmanship, the number of pigs farrowed and raised and their weight at weaning time together form the best measures we have of prolificacy and mothering ability of sows. They are particularly important since they have a tremendous influence on profitability. On the average, a sow will have consumed a total of 1,500 to 2,000 lb. of feed during the period between breeding and the date her litter is weaned. If this all has to be charged against a litter of only four or five pigs, the chance of eventual profit is small. In addition to number of pigs farrowed and raised, the weaning weight of the pigs is important since it has been definitely shown that the pigs which are the heaviest at weaning time reach market weights the soonest.

Daily gain from weaning to market weight is important because the fast-growing pig is on hand fewer days, thus requiring less labor and fewer days of shelter and exposure to risk of disease. Another important consideration is that rate of gain and efficiency of feed utilization are related, the correlation having been shown in several studies to be about +0.70. With this relationship and the difficulties of keeping feed records under practical conditions, most breeders will be content to select for efficiency of feed utilization indirectly through selecting fast-gaining pigs. In selecting primarily for rate of gain, there may be danger of selecting for excessive fatness since, as discussed later, these characters may be correlated to some degree.

As is to be expected, the estimates of heritability for various characters in swine (Table 52) show considerable variation from study to study but do show general trends. The heritability of litter size at birth is evidently low, only two of the nine estimates being over 22 per cent. Most investigators have found heritability of this important character to be less than 20 per cent. Three estimates of heritability of litter size at about weaning age range from 17 to 31.7 per cent, indicating that this character is likewise low in heritability. Similarly, weaning weight of litter is apparently low in heritability.

TABLE 52.—ESTIMATES OF HERITABILITY FOR VARIOUS CHARACTERS IN SWINE

Character	Heritability, %	Method used to determine heritability	Reference
Litter size at birth	17	Maternal half-sib litters	Lush and Molln (1942)
	10 17 18 34 44	Estimated from published reports of various workers	Lush and Molln (1942)
	13	Maternal half-sib litters	Hetzer *et al.* (1940)
	14.5	Average of 3 methods	Stewart (1945)
	21.7	Intrasire regression	Cummings *et al.* (1947)
	24	Average of 2 methods	Blunn and Baker (1949)
Litter size at weaning	17	Maternal half-sib litters	Lush and Molln (1942)
	22	Average of 2 methods	Blunn and Baker (1949)
	31.7	Intrasire regression	Cummings *et al.* (1947)
Litter size at 70 days	20	Maternal half-sib litters	Hetzer *et al.* (1940)
Weaning weight of litter	18	Maternal half-sib litters	Lush and Molln (1942)
	7.4	Intrasire regression	Cummings *et al.* (1947)
	37	Average of 2 methods	Blunn and Baker (1949)
Survival	40.3	Intrasire regression	Cummings *et al.* (1947)
Pig weight at 56 days of age	0	Intrasire regression	Comstock *et al.* (1942)
	15	Paternal half-sib	Baker *et al.* (1943)
	0	Paternal half-sib	Nordskog *et al.* (1944)
	13.6	Paternal half-sib	Krider *et al.* (1946)
Pig weight at 180 days of age	14	Intrasire regression	Comstock *et al.* (1942)
	20	Paternal half-sib	Whatley (1942)
	62	Intrasire regression	Whatley (1942)
	30	Intrasire offspring-dam correlation	Whatley (1942)
	40	Full sibs, not litter mates	Whatley (1942)
	30	Regression of variance to genetic relationship	Whatley (1942)
	23	Paternal half-sib and intrasire regression	Whatley and Nelson (1942)
	19	Line differences due to selection	Krider *et al.* (1946)
	23.9	Paternal half-sib	Krider *et al.* (1946)
Market score at slaughter	33	Average of 2 methods	Whatley and Nelson (1942)
Conformation score	20	Intrasire regression	Stonaker and Lush (1942)
Type of score:			
Within strains	38	Paternal half-sib	Hetzer *et al.* (1944)
Between strains	92	Paternal half-sib	Hetzer *et al.* (1944)

All estimates of the heritability of individual pig weights at 56 days of age are low, indicating that weight at that age is largely a function of the nursing ability of the sow rather than of the pig's own genes. After weaning, however, the pig's own genes evidently exert their influence, and heritability increases to possibly about 30 per cent at 180 days of age.

Heritabilities of various type and conformation scores average around 30 per cent in studies where only animals of basically similar types were studied, but in one study where strains of different types were considered, an estimate of 92 per cent for the heritability of type score was found. The latter figure probably explains why breeders have been able to alter hog types rather rapidly upon occasion in the past, while the figure of 30 per cent within strains indicates why further improvement often seems to come so slowly in a herd already fairly good.

In order to put the above figures in more practical terms, let us consider a hypothetical example. If the inheritance of these characters were assumed to be all due to additive gene action, if we assume that litter size weaned and litter weaning weight are each 20 per cent heritable, and 180-day weight and conformation each 30 per cent heritable, and that we have herd averages for the various items as indicated, then the progress to be expected from one generation of selection would be as shown herewith.

	Av. of herd	Selected individuals	Av. selection advantage	Heritability, %	Expected performance next generation
Av. No. of pigs weaned	6.0	6.6	+0.6	20	6.12
Av. litter weaning weight	180.0	198.0	+18.0	20	183.60
Av. individual 180-day weight	180.0	195.0	+15.0	30	184.50
Av. type score*	5	7	+2.0	30	5.6

* Graded on a scale from 1 to 9 with 1 being inferior and 9 excellent.

The selection advantages indicated for each character are approximately of the size it has been found possible to make in herds of the Regional Swine Breeding Laboratory when selections are made largely upon the basis of production records.

The gains expected for any one character are relatively small and, even if they were all attained genetically, environmental differences from year to year are great enough to make it difficult to know whether progress is being made until records have been kept for several years.

There are several reasons for believing that the figures given are themselves too optimistic when all factors are being considered at the same

time. The bases for this statement are: (1) Recent unpublished studies at several stations[1] participating in the Regional Swine Breeding Laboratory have shown that the expected advantages from selection have not been realized. These studies are complicated by the fact that most of the lines studied are being inbred and this may be depressing performance more than realized. Then, too, the studies cover a period of only a few years. (2) There is a continuous automatic selection for litter size which has apparently been going on for centuries without raising average litter size above its present modest average.

This last point is something which has apparently not been considered in previous animal-breeding texts and which may need a word of explanation. To understand this, it is necessary to differentiate between "average litter size raised" per sow farrowing and "average size of litter *in which raised*" for the pigs raised. To make this clear, let us consider an actual example of a group of 12 litters born to gilts in an inbred line on a Purdue University farm in 1948.

Size of litter (No. of pigs raised)	No. of litters	Total No. of pigs raised in litters of this size	Litter size × No. of pigs raised
8	1	8	64
7	1	7	49
6	5	30	180
5	2	10	50
4	1	4	16
2	2	4	8
Totals.	12	63	367

"Av. litter size raised" per sow farrowing = $^{63}/_{12}$ = 5.25

"Av. size of litter in which raised" per pig raised = $^{367}/_{63}$ = 5.82

If a person selected breeding stock from this group of litters entirely at random so far as litter size was concerned, he would be making a positive selection of 5.82 − 5.25 = 0.57 of a pig per litter over the average of that generation. This is, of course, due to the fact that the larger litters have more pigs available. The previously mentioned Regional Swine Breeding Laboratory study indicates that a high percentage of the selection practiced for litter size is of this automatic type.

It is possible that in breeders' herds animals from small litters are better grown and are therefore selected for breeding purposes with a resultant lack of positive selection for litter size. The fact that there

[1] Iowa, Nebraska, Missouri, Illinois, Indiana, Wisconsin, and Oklahoma stations. The data are now being summarized for publication by Dr. G. E. Dickerson of Missouri.

is by no means an absolute negative correlation between litter size and rate of development, together with the fact that many breeders have consciously selected for large litters, makes this seem unlikely.

If, as seems likely, litter size is failing to respond to selection as rapidly as it theoretically should, the reason is probably either (1) prolificacy depends to a certain extent at least upon "overdominance," with the best performers being heterozygous for a larger-than-average number of gene pairs, or (2) there is a negative correlation between prolificacy and certain other factors so that when we select for some of these, such as rate of gain, we indirectly select for smaller litters and override any actual positive selection we have made for litter size.

No positive evidence for "overdominance" has as yet been advanced with swine, although the possibility that it may exist cannot be overlooked. Dickerson and Grimes (1947) and Dickerson (1947) have presented convincing evidence that in the material with which they worked rapid gain was correlated genetically with (1) rapid fat deposition (r = around 0.60) and (2) low feed requirements ($r = 0.78$). The data strongly suggested that poor suckling ability may be caused by the same genes responsible for rapid fat deposition and low feed requirements.

Blunn and Baker (1947) working with a different herd of hogs found no significant genetic correlation (actually slightly negative, $r = -0.04$) between rate of gain and carcass fatness as estimated from back-fat thickness. No data on feed requirements were kept in their experiment. Winters *et al.* (1949) in an experiment where rate of gain was controlled by limiting feed intake during certain periods of the feeding period in some lots found that the slower gaining lots had lower feed requirements and produced leaner carcasses. They rightly point out that genetically slow rate of growth may be quite a different thing from environmentally controlled slow growth. They also point out on the basis of other data from their swine-breeding project "that a high rate of gain, economy of feed utilization, and a quality carcass can be combined."

Quite aside from the experimental data on the subject, a priori reasoning (always a dangerous procedure!) might be taken as indicative of a negative relationship between maternal ability and rapid fattening. Bacon hogs are commonly reputed to raise larger litters than most lard breeds. Likewise in cattle, no one has yet succeeded in combining the best beef type with maximum milking ability.

If there is a strong negative association between rate and economy of gain and maternal ability, the increased use of crossbreeding or crossing of inbred lines for commercial production is suggested. Dickerson (1947) makes the following suggestion[1] from his data:

[1] *Iowa Agr. Expt. Sta. Res. Bul.* 354, October, 1947.

It suggests that maximum performance can be secured only through judicious crossing of different strains of swine. For example, sows of a cross that has exceptionally good milking ability and prolificacy mated to boars from a strain that excels in rate and economy of post-weaning gains would give maximum litter performance.

Regardless of whether this association exists, it is far from absolute and few lines or strains of hogs are being developed by selection based on one character only. The economics of producing breeding stock make it probable that a line extremely deficient in maternal ability but exceptionally good in growth rate or vice versa could not be profitably used. Thus, we will have to continue selecting animals for reasonable excellence in all qualities. It is true, however, that existing swine breeds differ significantly in certain characteristics, with some being strong in one character and some in another. These differences may depend upon chance fluctuations in gene frequency or upon the type of selection which has been practiced in the various breeds. As inbred lines are developed, they likewise differ from each other. Judicious crossing will take advantage of these differences and may prove to be the method which will give maximum performance.

Even if reasonably high merit in most characteristics is accepted as the aim in swine breeding, a question yet to be answered is that of what system of selection will result in maximum total progress over a period of several years or generations. Should selection be solely for one trait until it is improved, then for a second until it is improved, etc., until finally all characters have been improved to the desired levels? Or should selection be made simultaneously for all desired traits by using some index of net merit arrived at by adding into one figure the credits or penalties given each animal for its superiority or inferiority in each trait? Finally, should a method be used in which all traits are considered, but animals are culled if they do not reach a certain level for each trait regardless of excellence in other traits? Terming these the "tandem," "total score," and "independent culling level" methods, respectively, Hazel and Lush (1942) arrived at the conclusion that the tandem method of selecting first for one thing and then for another could be expected to be considerably inferior to either of the other two methods. The total-score method of selecting for several traits simultaneously should be superior to the method of independent culling levels. The latter may be useful in cases where some culling has to be done before all traits can be evaluated.

In spite of the admittedly slow rate of progress usually made in selecting swine, there is ample evidence that our present hogs show marked

improvement in growth, fattening ability, and other characters over their wild ancestors, thus showing that selection can be effective in bringing about improvement.

The best data showing definite improvement in swine over a period of years come from the records of animals fed out in the testing stations in Denmark as part of the swine progeny-testing system in that country.

The Danish system of swine breeding, as summarized by Lush (1936), is based upon a group of state-recognized breeding centers, where a high percentage of the boars used for commercial production in the nation are produced. The breeding centers are visited twice annually by a committee representing farmers' organizations and cooperative bacon factories and scored for numerous items including type and prolificacy of breeding stock, management and general appearance of farm, and health of animals. Each year the breeding centers are obligated to send enough test litters of four pigs each to average two pigs per sow in the herd to testing centers. The test litters are fed out under standard conditions and slaughtered at about 200 lb. live weight. Records are kept of rate of gain, efficiency of feed utilization, and several carcass measurements and scores.

Annual reports are issued which include the above information for each center. These reports are designed to serve as a guide for the purchase of breeding stock and the establishment of breeding programs.

The first of the testing stations was established in 1907, and the work is still progressing under a plan which has changed but little since its inception, except for an interruption in the First World War.

The following figures, calculated in some cases from graphs presented by Lush (1936) and in other cases from graphs and figures presented by Clausen (1949), indicate some important changes which have taken place in the performance of Danish Landrace pigs fed out at the testing stations:

	1909–1910	1924–1925	1947–1948
Av. daily gain, lb.	1.18	1.32	1.46
Av. feed required per unit gain	377	357	319
Av. age at 20 kg. live weight, days	......	69	74
Av. age at 90 kg. live weight, days	......	186	180
Class 1 bacon sides	......	40 %	90 %

Detailed data (Clausen, 1949) indicate that progress in lowering feed requirements per unit of gain has been slight during the past dozen years or so. The figures show that increases in rate of gain while on test have been accompanied by increases in age at 20 kg. live weight. This suggests

that selection for rapid gains on test may result in indirect selection for lowered milking ability in sows and thus for lower gains in pigs during the nursing period. Although rate of gain on test has increased by 11 per cent since 1924–1925, the decrease in age at 90 kg. live weight has been only about 3 per cent. In spite of this possible antagonism, it must be remembered, however, that the decrease of 6 days in age at 90 kg. live weight represents a real gain.

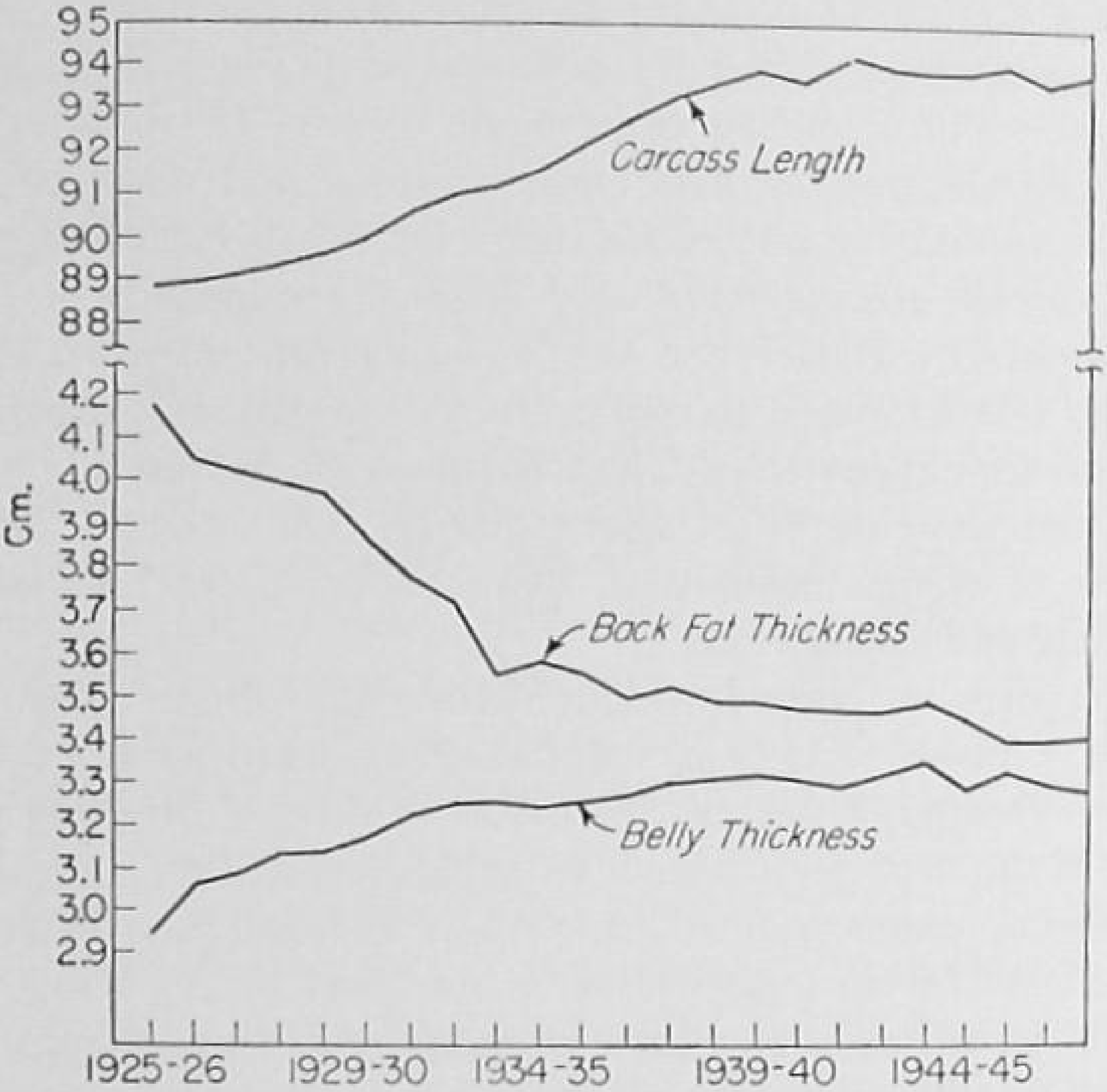


FIG. 196.—Graph showing trends in carcass length, back-fat thickness, and belly thickness in carcasses of Danish Landrace hogs fed out and slaughtered in testing stations in the Danish swine progeny-testing program. (*Redrawn by T. W. Perry of Purdue University from graph presented by Clausen,* 1949.)

The accompanying figure, adapted from Clausen (1949), shows that progress has been made in increasing body length, increasing belly thickness, and decreasing back-fat thickness. Progress during the past few years has not been so rapid as earlier, however. Doubtless this fact is an illustration of the principal that progress becomes more difficult in populations already greatly improved by selection.

Regardless of whether progress is becoming slower or whether some traits may be somewhat antagonistic to each other, real progress has been made in improving the Danish Landrace hog while this program has been in operation. The Yorkshire breed, maintained in smaller numbers than the Landrace, has changed in a roughly parallel fashion. Since the reports serve as only a guide to breeders, and since management

of the test litters has undoubtedly improved over the years (although known changes in rations or management are slight), it is impossible to determine how much of the improved performance can be attributed to genetic improvement resulting from the program.

Several other European countries and Canada have progeny-testing programs which are carried on under plans more or less similar to the one in Denmark.

In the United States production testing on an organized basis has been slower in developing, but several programs initiated during the past 20 years indicate that American breeders are coming to a realization of the

FIG. 197.—Ring Gold Lady Dora PR149, 753956, the first sow of any breed to produce eight qualifying litters in a P.R. program. Shown here with her sixth qualifying litter, the 10 pigs of which sold at auction for a total of $4,365. (*Courtesy of Hampshire Swine Registry Association, Peoria, Ill.*)

need for such procedures. Active efforts are being made to devise programs which will be practical with the huge hog population and under the management systems used in swine production here.

In 1938 the United Duroc Record Association initiated a program of "Production Registry" which is designed to give recognition to sows having the ability to farrow and raise large litters and nurse them properly to weaning. Recognition is also given to boars. Most of the other breed associations developed somewhat similar programs during the following years under rules which varied in some particulars. In 1946 all the associations united in adopting a single set of rules which (as changed somewhat in 1948) are as follows:

I. Farrowing reports.

Farrowing reports on nominated litters must be witnessed by one disinterested party of unquestionable standing in the community to verify size of litter and earmarking of litter. This farrowing report must be sent to the breed record association office within 5 days after the farrowing date.

II. 56-day weighing reports.

All nominated litters are to be weighed between 51 and 61 days of age and reported to the breed record association within 3 days after pigs are weighed. All litter weights will then be calculated to a uniform 56-day basis.

This 56-day weighing must be witnessed by one official, other than the owner of the litter, such as a county agent, 4-H Club agent, vocational agriculture instructor or supervisor, college livestock extension specialist, cow tester, director, or representative of the party designated and endorsed by, previous to the weighing, one of the aforenamed officials. It shall also be the duty of the official witness to check the accuracy of the scales used for the weighing.

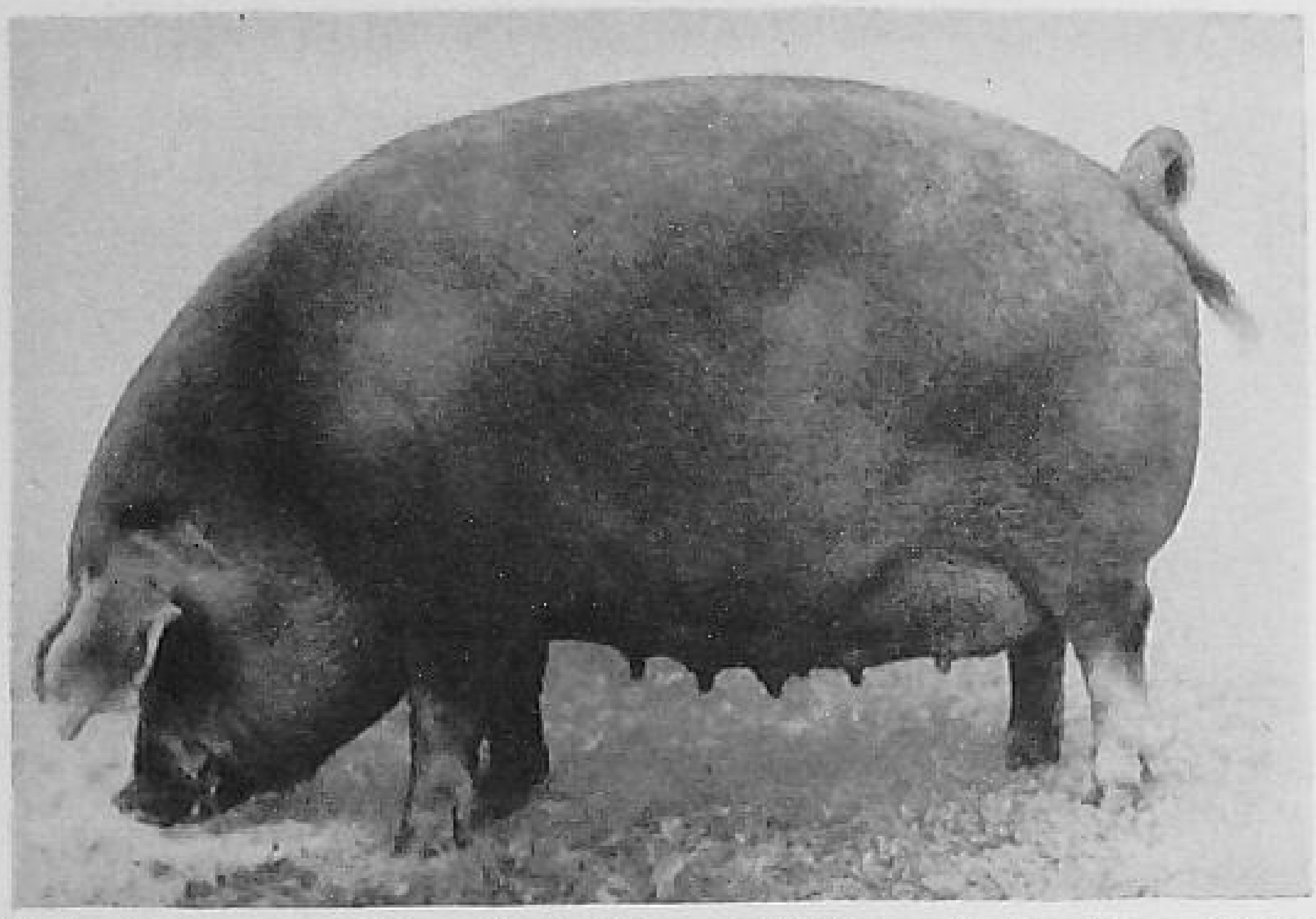


FIG. 198.—A P.R. Duroc sow, New Era's Type 185962. At the time of her death in 1946 she had raised 116 pigs in 12 litters for a lifetime average of $9\frac{2}{3}$ per litter. As well as being outstanding from a production standpoint, she was a noted show sow, being named reserve All-American aged sow in 1943. *(Courtesy of United Duroc Record Association, Peoria, Ill.)*

III. Qualifying litters.

A Production Registry qualifying litter shall be as follows:

A. For sows over 15 months of age at farrowing:

To raise, without the aid of a nurse sow, 8 or more pigs to an official 56-day litter weight of at least 320 lb.

B. For gilts (15 months of age or younger at farrowing time):

To raise, without the aid of a nurse sow, 8 or more pigs to a 56-day litter weight of at least 275 lb.

IV. Qualifying sows.

Sows will be officially admitted in the respective breed association Production Registry after having raised two qualifying litters. However, recognition for the first qualifying litter of any sow can be indicated on pedigree certificates where her name appears by affixing a star to her registry number. Production Registry sows will be classified according to the number of qualifying litters raised, such as 2-star, 3-star, etc.

V. Qualifying boars.

A boar may qualify for official Production Registry as follows:

A. When he has sired 15 or more official PR qualifying litters. Recognition for this honor will be designation as a PR Boar.

B. When he has sired five 2-Star PR daughters, or ten 1-Star PR daughters or an equivalent combination of both. Recognition for this honor will be designation as a 1-Star PR Boar. (In computing an equivalent combination each 1-star daughter will count *one point* and each daughter with two or more stars will count *two points*, the required total for any combination being *ten points*.)

C. When a boar has qualified once on the record of his PR daughters he may qualify for another star for each additional ten points on the basis of PR daughters, points to be calculated as in (*B*) above.

Entry blanks can be secured from the respective breed associations. Starting from small beginnings, the program has made steady progress, although as yet including only a small fraction of the sows of any breed. Following is a tabulation of the number of litters nominated and qualifying in 1948 in two of the major breeds:

Breed	No. of litters nominated	No. of litters qualifying	% qualifying
Duroc	2,476	747	30.2
Chester White	128	43	33.6

This program represents a constructive start on the difficult problem of getting production records on purebred swine. Some may be inclined to criticize it for not getting enough data, but in order to secure participation, it must be kept simple at least until experience dictates the necessity of more extensive records. The value of weaning weights as indicators of genetically influenced growing ability is not clear. It is an established fact that the biggest pigs at weaning grow faster thereafter and reach market weights sooner than lighter weaning pigs. It is possible that the same genes affect the growth rates of pigs during the pre- and postweaning periods. However, available evidence indicates that weaning weight is very low in heritability—apparently being largely determined by the maternal ability of the dam. Daily gain at any stage of a pig's life is dependent upon size already attained, the heavier pig making a bigger gain. Comstock *et al.* (1942) found that weaning weight was correlated with rate of gain from weaning to 200 lb., but not with rate of gain from 50 to 200 lb. Thus, the heavier pig at weaning apparently reaches market weights sooner not because of inherently greater growing ability, but because it (1) is in a more advanced phase of the growth curve at weaning and (2) has already attained a greater percentage of the final weight.

From the standpoint of the practical hog producer, however, age at market weight is the important consideration. Since heavy weaning pigs reach market weights in fewer days, selection for them may be

effective even if it is more directly selection for sow maternal ability than for gaining ability as such.

It is well at this point to introduce a word of caution in order that swine breeders may not be tempted to make the same mistake that our dairy-cattle associations made with their AR testing. The mistake that practically spoiled all the good that might have come from this system was the fact that a man could test as many daughters of a bull as he wanted to. Naturally, the best daughters were tested, the poor ones not. This gave a very distorted picture of the breeding worth of hundreds of bulls. Any bull can be made to look good if the breeders test only a few of his best daughters. Likewise, any boar can be made to look good if they put only a few of his very best daughters into PR testing. When this is done, they completely defeat the very purpose of the system, which is to determine the genetic breeding worth of the animals. Thus, all a sow's litters should be considered in evaluating her, and the records of all a sire's daughters that farrow should be used in evaluating him.

At least one breed association is developing a program of herd testing in which weights are taken on all litters in the herd, not only at 56 days of age but at six months. This is a most constructive step and overcomes the danger of selective testing inherent in the PR program. Some breeders are now following the commendable practice of weighing all pigs and publishing the records made, be they good or bad, as a part of the pedigree in sale catalogues. An example of an actual pedigree printed in the catalogue of a recent purebred Hampshire sale is given in Fig. 199.

Another word of caution should be introduced against undue forcing of litters because of the advertising values sometimes attached to extreme weight records. Records made under practical conditions will be of much greater value in assessing the genetic worth of the animals. The primary purpose of "Production Registry" is to reduce the number of small litters weighing less than 275 lb. and to increase the number in the commendable range of 350 to 450 lb.

Another significant development during the past few years has been the growth of sow-testing programs in various states. Probably the most highly organized of these is the Wisconsin Swine Selection Cooperative. This program is designed to provide information which will aid the breeder in making intelligent selections from his herd for breeding purposes.

The breeder ear-notches each pig individually at birth and records litter size. The cooperative furnishes forms for keeping records and employs field men to aid the breeders taking weights of pigs at approxi-

mately 154 days of age. The weight records are sent to the University of Wisconsin where they are adjusted to 154 days of age. An index is then calculated for each pig and the records returned to the breeder in time for him to use the index in selecting breeding stock.

LOT No. 24 **LITTER No. 62**

CONNER VERBENA

GILT, Tag 2501, 56 Day Weight 30.6 lbs., Dinner Plates 14

(Pedigree of Litter 62)

Farrowed Jan. 27, 1948
Pigs Farrowed 13
Pigs Raised 9

Average birth wgt. 3.1 lbs.
Average 56 day wgt. 30.49 lbs.
Bred by Conner Prairie

CONNER TOP DECK 361355
14 litters av. 9.43 pigs born
14 litters av. 7.1 pigs raised
Average birth wgt. 3.19 lbs.
Average 56 day wgt. 32.69 lbs.

- CONNERS COMMANDER 348641
  4 litters av. 8.75 pigs born
  4 litters av. 5.5 pigs raised
  Average birth wgt. 2.39 lbs.
  Average 56 day wgt. 28.85 lbs.
- CONNER ALBRIGHT 879126
  5 litters av. 10.6 pigs born
  5 litters av. 6.8 pigs raised
  Average birth wgt. 3.03 lbs.
  Average 56 day wgt. 33.88 lbs.

CONNER SILVER STAR 896490
3 litters av. 10.66 pigs born
3 litters av. 9.33 pigs raised
Average birth wgt. 3.04 lbs.
Average 56 day wgt. 30.9 lbs.

- SOUTHWIND ROCK & RYE 303037
  27 litters av. 9.1 pigs born
  27 litters av. 6.26 pigs raised
  Average birth wgt. 3.09 lbs.
  Average 56 day wgt. 31.67 lbs.
- MORNING STAR 785214
  7 litters av. 11.57 pigs born
  7 litters av. 10.29 pigs raised
  Average birth wgt. 3 lbs.
  Average 56 day wgt. 26.15 lbs.

FIG. 199.—Pedigree of a gilt sold in a recent Hampshire auction in which production records of all animals were given. (*Courtesy of Conner Prairie Farm, Noblesville, Ind.*)

As an example of the index, let us assume we have a pig—one of a litter of eight, all of which were raised to five months—and that this pig weighs 175 lb. at five months:

	Points
1 point allowed for each pig farrowed (up to 12)	8
2 points allowed for each pig raised to 5 months	16
Total litter weight at 5 months divided by 100 (let us assume the litter weighed 1,300 lb.)	13
7/10 point for each pound over 75 lb. for the individual pig at 5 months. (Our 175-lb. pig at 5 months would be scored 100 × 7/10)	70
Pig index	107

PURDUE UNIVERSITY
DEPARTMENT OF ANIMAL HUSBANDRY
Individual Sow Record

Breed: ________ Name and Registry No. ________

Ear Notch R L Herd No. ________

Pedigree:	
Sire: ________	________
Br. by:	________
Dam: ________	________
Br. by:	________

Date farrowed ________	Date of disposal ________
No. in litter ________	Reason for disposal ________
No. raised ________	________
Av. 56 da. wt. ________	________
Own 56 da. wt. ________	Buyer ________
Av. 180 da. wt. ________	________
Own 180 da. wt. ________	________
Bred by ________	Price ________
Purchased from ________	
________	
Date ________	
Price ________	

*Score at 225 #

Vigor, health, and thriftiness	________
Quality	________
Length of body	________
Details of conformation	________
Animal as a whole	________
Grade	________
Defects	________
Total	________

Remarks about conformation:

Photograph

Herd No. ________

* Points from 1 to 9 with 9 a perfect score except in the case of length of body where 9 merely means a long body.

(OVER)

FIG. 200.—An example of a permanent record sheet for a sow. One side of an individual sow record sheet giving pedigree and other information regarding a sow before she reached breeding age. (*Courtesy of Dr. J. A. Hoefer, Purdue University, Lafayette, Ind.*)

Production record of sow no. ____________

RECORD OF LITTERS PRODUCED

Litter No.	1	2	3	4	5	6
Sire						
Farrowing date						
No. services for this conception						
No. farrowed						
Total birth wt.						
Number at 21 days						
Number at 35 days						
Number at 56 days						
Total wt. at 56 days						
Ave. weaning score						

Notes: (health of sow, fertility record of boar to which bred, etc.)

FIG. 201. Reverse side of the sow record sheet shown in Fig. 200. A summary on one sheet of all litters a sow has produced makes it easy to evaluate her productivity. *(Courtesy of Dr. J. A. Hoefer, Purdue University, Lafayette, Ind.)*

Programs of the type described above are very helpful in expediting the necessary book work in a production-testing program. Then, too, they have an official standing which increases their value somewhat over and above the value of private records.

The keeping of personal records is to be urged, however, if suitable organized programs are not available. These records need not be elaborate, but should include pedigree records on each litter, records of the number of pigs farrowed and weaned, and weights of the individual pigs at weaning (usually 56 days of age) and at some later time, preferably

TABLE 53.—FACTORS FOR CONVERTING PIG WEIGHTS TO STANDARD AGES OF 56 AND 154 DAYS

Factors for converting individual pig weights to 56 days*		Factors for converting individual pig weights to 154 days†	
Age	Factor	Age	Factor
47	1.2812	145	1.108
48	1.2424	146	1.095
49	1.2059	147	1.082
50	1.1714	148	1.070
51	1.1389	149	1.058
52	1.1081	150	1.046
53	1.0789	151	1.034
54	1.0513	152	1.023
55	1.0250	153	1.011
56	1.0000	154	1.000
57	0.9762	155	0.989
58	0.9535	156	0.978
59	0.9318	157	0.968
60	0.9111	158	0.957
61	0.8913	159	0.947
62	0.8723	160	0.937
63	0.8542	161	0.927
64	0.8369	162	0.918
65	0.8200	163	0.908

* Calculated from the formula

$$Y = Z\left[\frac{41}{X - 15}\right]$$

where Y = corrected weight
Z = actual weight
X = age in days

† Calculated from the formula

$$W = Z\left[\frac{142.5}{0.0032143X^2 + 0.58X - 23}\right]$$

where W = corrected weight
Z = actual weight
X = age in days

about five months of age. Factors have been worked out by Whatley and Quaife (1937) and Lush and Kincaid (1943) for adjusting individual pig weights to 56 or 154 days of age, respectively. These make it possible to weigh several litters at once and convert all records to a standard age for use in comparing the records of various individuals.

Assuming production records are being kept, the breeder is faced with the problem of how to evaluate them in selecting breeding stock for retention in the herd. How much emphasis should be put on weight

PURDUE UNIVERSITY
Animal Husbandry Department
Litter Record, Farrowing to Weaning

Sow Number______ Litter Number______
Sow's Sire______ Sire of Litter______
Sow's Dam______ Breeding Date______
Date of birth, sow______ Farrowing Date______
Litter______ (1st, 2nd, etc.) Date Vaccinated______
Sow's weight: at breeding______ Date weaned______
at 100-112 days______
at weaning______

Sow's general appearance
at farrowing: Good, Medium, Poor
No. good teats: R____ L____
at weaning: Good, Medium, Poor
No. functioning teats: R____ L____

Litter's general appearance
at farrowing: Good, Medium, Poor
at weaning: Good, Medium, Poor

Pig No.	Sex	Birth Weight (lbs.)	Weaning (56 days Date) Act. wt. at ____ days	Calcul. 56 days wt.	No. Nipples	Remarks, defects, abnormalities, disposal

FIG. 202.—An example of a record sheet used to keep records on a litter of pigs to weaning age. (*Courtesy of Dr. J. A. Hoefer, Purdue University, Lafayette, Ind.*)

for age, how much on litter size, how much on litter weaning weight, how much on body type, etc.? No one answer can be given to this question. Hazel (1943) in an analysis of the factors involved in constructing selection indexes, pointed out that the emphasis which should be placed upon the different characters depends upon (1) the relative economic importance of the various traits, (2) the variation in each trait, (3) the heritability of each trait, and (4) the phenotypic and genetic correlations between each pair of traits. Obviously, these constants may vary from herd to herd and even in the same herd over a period of time. Using data from the Iowa Station swine herd of inbred Poland Chinas,

Hazel employed a multiple correlation method to construct selection indexes. Using information on the pig's own 180-day weight (W), the pig's own conformation score at market weight (S), and information on litter size and weaning weight expressed as "productivity of the dam" (P), he arrived at the following index:

$$I = 0.136W - 0.232S + 0.164P$$

An apparently slightly more efficient index including terms for the average weight and score of the pigs in the litter was constructed. Since the coefficients of these terms vary with the number of pigs per litter, this index does not lend itself well to presentation as an illustration.

An interesting feature of Hazel's index is the negative attention assigned to score. This is due to the fact that weight and score are phenotypically correlated with the pigs biggest for their age also tending to receive the highest scores. Thus, selection for heavy pigs automatically selects for better type, and the type score can be discounted.

It is not known whether the values given by Hazel would apply to other herds and breeds of swine. From his analysis and from other information, it appears probable, however, that as long as present marketing practices prevail in the United States considerably more attention should be paid to the items measuring sow productivity and weight for age than to conformation.

Under usual conditions, the performance of an animal itself is the best *single* indication of its genotype. Thus, for characters which can be measured in the individual, selection based on individuality should be practiced at least to the extent that no individuals of below-average merit should be kept, regardless of the performance of relatives. Pedigree and family selection are a useful supplement to individual selection, and in selecting young animals for such things as prolificacy and nursing ability, this type of evaluation is the only type possible. The general plan of retaining the best individuals from the best families appears to be sound in hogs.

Lush (1947) in a searching analysis of the relative value of individual and family selection pointed out that if either method is *absolutely ineffective the other will be also.* He found that a combination of individual and family selection is at least equal to either type of selection alone and is distinctly superior when (1) genetic relationship within family is moderate and the phenotypic correlation within family is much smaller but well above zero, and (2) when the phenotypic correlation is distinctly larger than the genetic relationship within family. The latter case is interesting since for this to occur family averages must depend more upon environmental conditions peculiar to each family than upon genetic

similarity. Under these conditions family averages play a negative part in combination selection. Family selection is most necessary for those traits in which members of the family resemble each other least, *i.e.*, for traits which are low in heritability.

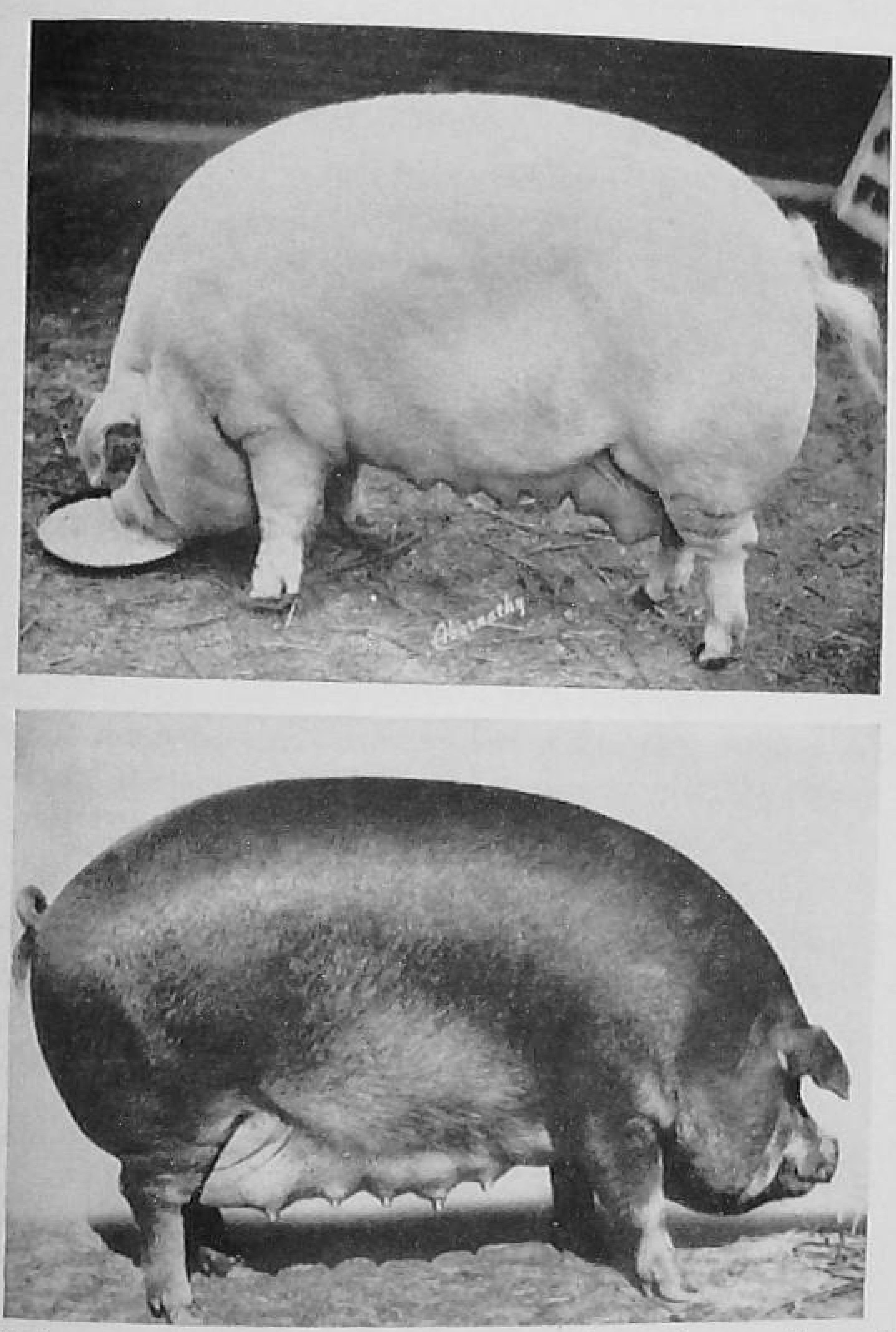


FIG. 203.—Modern sow types. Chester White sow (above) Supreme Fancy 2nd, grand champion 1947 Illinois State Fair. Owned and shown by Harry Brett, Decatur, Ill.; and Duroc sow (below) Tiptop Princess 3rd, grand champion 1948 Nebraska State Fair. (*Courtesy of Chester White Swine Record Association and Duroc Record Association.*)

Due to the approximate doubling of the generation interval, progeny testing (considered here in the strict sense as being the plan followed in which young sires are progeny-tested on outside females before being used in the herd) appears to be of limited usefulness with swine (see Dickerson and Hazel, 1944b). Progeny performance should, however, be a major consideration in determining which boars to keep for use in

a herd a second or third breeding season. Sows to be retained should be selected on the basis of the performance of a first litter. The number of pigs farrowed and weaned and their growth to weaning are largely maternal characters. Thus, selection for them is really individual selection superimposed upon the family selection by which the sows were first selected as gilts. After weaning, the performance of a pig depends to an increasing extent upon its own genes. Thus, selection of sows upon the basis of postweaning performance of a first litter is partially progeny-test selection.

Dickerson and Hazel (1944a) have arrived at the decision that maximum progress can be made in a closed herd or a breed if approximately one-third to one-half of the sows are kept for a second litter and a *very few* of those which performed best in their first two litters are retained for a third and fourth.

A Regional Swine Breeding Laboratory was established with headquarters at Ames, Iowa, in 1937, under the authority of the Bankhead-Jones Act of 1935. According to the director, Dr. W. A. Craft,[1]

> The principal objective of the laboratory is to discover, develop, and test procedures of breeding that will result in improvement of swine. The following four phases of study are involved: Systems of breeding, measures or standards of appraising hogs and their carcasses, heritability of various characters, and physiology of reproduction. Emphasis is being placed on productiveness of sows, growth rate of pigs, economy of gains, vitality, and desirability of carcasses.

At the present time the state experiment stations in the Middle Western region have active programs in this project, and several other states are carrying on work of a similar nature and cooperating informally with the laboratory. The general procedures used[2] are as follows:

> A promising supplement to conventional breeding practices that is being studied at the laboratory is the development of inbred lines combined with selection for productiveness of individual animals. This permits selection from different lines of breeding, use of inbred boars for top crossing on noninbred stock, and hybridizing inbred lines within and between breeds. Inbreeding to some degree is necessary to form distinctly different lines of stock, especially within breeds; it expedites the forming of lines that differ widely in their heredity. Production recording is being practiced as it helps in locating not only the superior lines but also the individuals and litters within lines that have the best heredity.

Systems of breeding including various degrees of inbreeding of 3 to 5 per cent per generation (four sires in a herd closed to outside blood), of 6 to 7 per cent per generation (two sires in a herd closed to outside blood),

[1] *U.S. Dept. Agr. Misc. Pub.* 523, July, 1943.
[2] *Ibid.*

of 11 to 12 per cent per generation (one sire in a herd closed to outside blood), and of somewhat greater intensity in a few lines carried for a few generations by full sib matings are being studied. Inbreeding is being carried on both within established breeds (33 of the present inbred lines) and within new strains produced by crossing two existing breeds (4 of the present inbred lines).

Results to date indicate that, on the average, some depression in productivity occurs with increases in inbreeding, in spite of continuous selection for productivity. This is more serious in some lines than in others. Dickerson *et al.* (1947) using data from four Regional Swine Breeding Laboratory herds showed *average* decreases per 10 per cent increase in inbreeding of 0.2, 0.4, and 0.5 pigs per litter at birth, 21 days, and 56 days of age, respectively. Average 56-day weight per pig was not affected, but there was a 3½-lb. per pig decrease in 154-day weight for each 10 per cent increase in inbreeding.

The past few years most stations involved in this work have been testing inbred lines in crosses with each other and in top crosses with noninbred stock. A few of these results were quoted in a previous chapter. A recent statement by Director W. A. Craft[1] summarizes these results:

> Crossing of three or more lines restored the losses in all traits; in some cases crossing of three or more lines produced increases in most of the traits studied as compared to the performance of the parent lines before inbreeding or as compared with noninbred stock used in some trials as controls. Some, but not all, inbred boars have sired litters which exceed, in weight and numbers of pigs, litters by noninbred boars at 5 or 6 months of age; some, but again not all, boars from crosses of two inbred lines have sired litters which beat litters by other noninbred boars at 5 or 6 months of age; crossline sows have proved to be good pig raisers; crosses of inbred lines of different breeds have shown more hybrid vigor than line crosses within a breed; genetic divergence of stock of different breeds seems to provide gene patterns differing enough to produce more hybrid vigor than lines related to each other such as is the case when they are of the same breed. Study of data completed recently for 70 litters of line crosses within the Poland China breed compared with 72 litters of crosses of lines between breeds shows a difference of 0.66 pigs at birth, 4.2 pounds per pig at weaning and 12 pounds per pig at 5 months in favor of the lines of different breeds. Hybrid vigor appears to be as real in pigs as in corn, but there are economic problems involved in obtaining it which are more difficult to overcome than is the case in corn.

The lines produced by mild, medium, and intense inbreeding appear to differ little in average merit as inbred lines or in their usefulness in crosses. Since rapid inbreeding results in a considerable saving in time,

[1] Quoted from a speech given in April, 1948, at the University of Illinois Swine Day.

it now appears that the most feasible method of producing inbred lines is to start many small inbred lines and inbreed intensively at first. The least promising lines can then be discarded and the remaining ones tested in crosses.

Although several of the inbred lines produced thus far in this study appear to have real value and may in themselves exert a beneficial influence on American swine production, the work of the laboratory must be considered primarily a study of methods. As promising methods are developed, breeders are adopting them and can be expected to develop better lines than the relatively few developed thus far by the experiment stations. If the methods used continue to show promise, this program can be expected to exert a considerable influence over future swine-breeding practices.

Selection in Sheep.—In colonial America, sheep were grown almost entirely for the purpose of producing wool. This led shortly to the creation, from Spanish Merino importations, of the American Merino breed, which became very numerous along the Eastern seaboard, with Vermont at that time the leading state in number of sheep, owing in large measure to the influence of William Jarvis, who had a farm at Weathersfield, Vt., and at the time was serving as American consul in Lisbon, Portugal. The wool clip in the early colonies was only 2 or 3 lb. per animal per year, but through selection and improved feeding and management it has been continuously raised to an average level of 7 or 8 lb. for the present sheep population (all types) of the United States.

From the Vermont Merino, there were later developed the various Delaine Merinos for the purpose of producing a fine wool of sufficient length for combing. Most of the numerous Merino breed associations that had sprung up were merged in 1906 into the American and Delaine Merino Record Association, with three other smaller associations still existing. Merino type varies from a small thin animal of poor carcass quality but heavily wrinkled and producing a fine, dense, heavy fleece of short wool (Type A), to a larger, fairly heavy, and low-set animal producing a good carcass but generally lacking wrinkles and with a heavier but less fine and dense fleece (Type C or Delaine), and a third intermediate form (Type B).

From Spanish Merino foundations, the French developed a fine-wool strain of sheep, the Rambouillet, of much greater size than the American Merino. Many of these animals were brought to America about the middle of the nineteenth century, and for a time they were a very popular breed. Interest then declined, to be revived about 1890. The Rambouillet is a large animal producing a heavy, dense fleece. As with the American Merino, there are variations in amount of skin wrinkles and

at some shows the animals are divided into B and C types. They were brought to America to serve primarily as wool producers. In recent years, greater attention has been paid to fleshing qualities, more by some breeders than others, but the carcasses are not of so high a grade generally as those from the Down breeds. This breed has been called the most typical dual-purpose breed in America, yielding something in

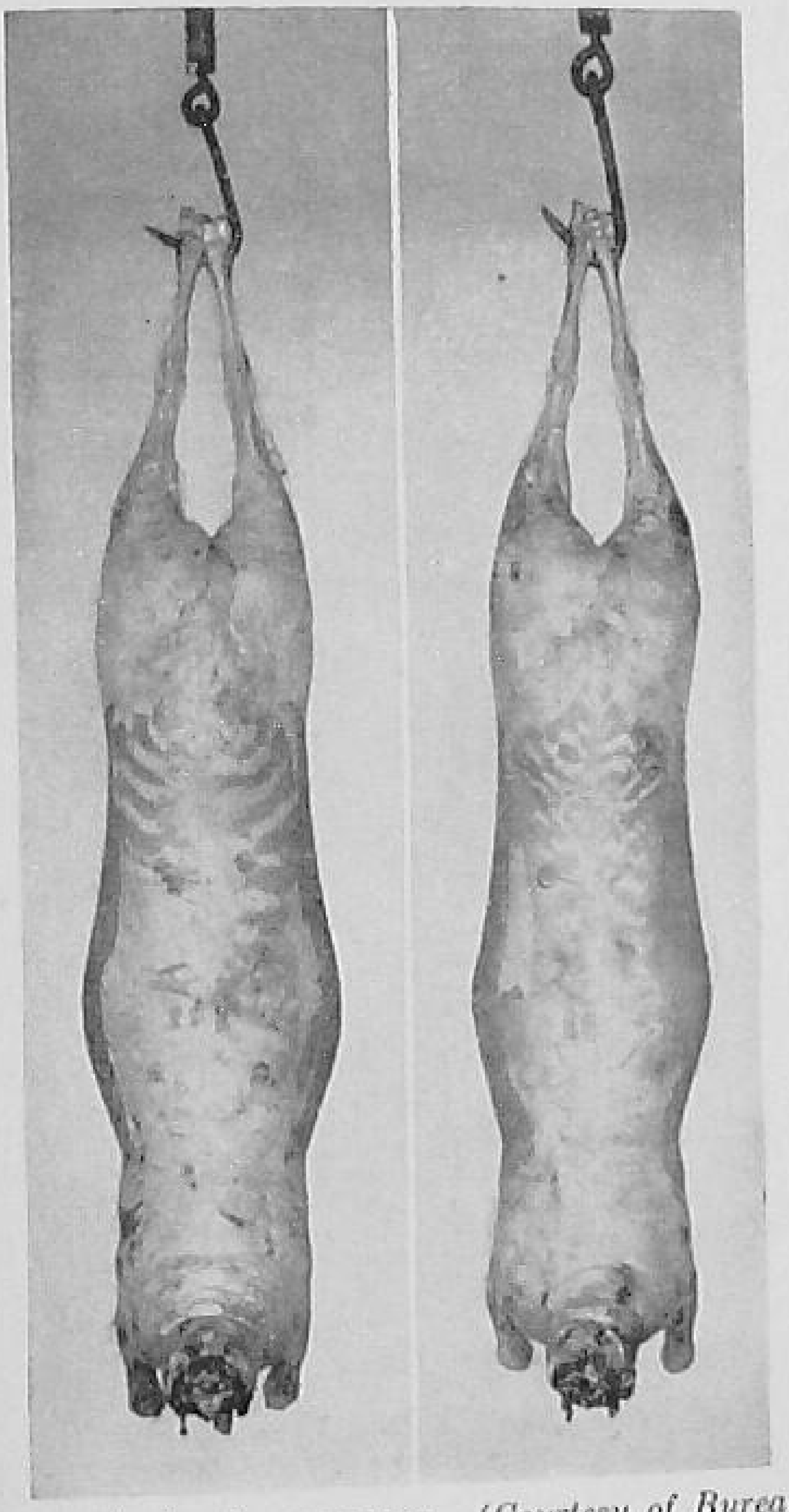


FIG. 204.—Different types in lamb carcasses. *(Courtesy of Bureau of Animal Industry, U.S. Department of Agriculture.)*

density and fineness of fleece to the American Merino and to the Down breeds in quality of carcass. Under these conditions, we would expect to find wide degrees of variation in the breed.

Robert Bakewell, the noted English livestock breeder of the eighteenth century, greatly improved one of the long-wool breeds, *viz.*, the Leicester. He devoted his major attention to fleshing or fattening qualities and quite neglected consideration of wool. The result was a fairly large breed of sheep with rather long and coarse wool and a carcass of a coarse grain, which when finished was overlaid with several inches of fat. To a

greater or less extent, these qualities are found also in the other long-wool breeds, Cotswolds, Lincolns, and Romneys. The long-wool breeds were created, therefore, primarily to serve as meat animals supplying the large, fat legs and roasts then in demand. In recent years, more attention has been paid to wool, and attempts have continually been made to improve the quality of carcass in these breeds. The fine-wool breeders generally pay particular attention to fleece, less to carcass qualities. The long-wool breeders, on the other hand, pay more attention to carcass, less to fleece.

The various "Down breeds" of sheep, Southdown, Shropshires, Oxfords, Hampshires, etc., have been developed to fill the void between the fine-wool and long-wool breeds. They are, in a sense, a happy medium between two extremes with the very great added advantage of producing very superior carcasses from the standpoint of quality. The various Merinos and the Down breeds have been bred and kept relatively pure in the East and Midwest. In the range country farther west, the foundation females were largely grade Rambouillet ewes. On these ewes, there have been used all the types of American and Delaine Merinos and Rambouillet rams. Later, rams from the long-wool breeds were used, particularly Cotswolds and Lincolns, in the attempt to improve size and fleshing, and rams from the Down breeds were used to try to improve carcass quality still further. Finally the use of long-wool rams on fine-wool ewes in the attempt to get good sheep from the standpoint of both wool and mutton led to the formation of the Corriedale breed in New Zealand (imported to the United States in 1914) and the Columbia, Panama, Targhee, and Romeldale breeds in the United States.

As can be seen from the above discussion, there are a great many types of sheep in existence. Sheep are raised in the United States under a greater range of environmental conditions and management systems than is true of any other class of farm animal. The first job of the sheep breeder is, therefore, to select the type and breed of sheep best adapted to the conditions under which operations will be carried on and where breeding stock will be sold. It may well be that more breeds are needed to fill needs in certain areas.

The second task of the breeder is to improve the productivity of the type of sheep selected. Although in former years many sheep were kept almost exclusively for wool production with aged wethers often being run for this purpose, the sheep industry is today almost universally on a dual-purpose basis, *i.e.*, both wool and meat animals (usually lambs) are major products, with the relative importance of the two varying considerably in various areas. For example, in the semiarid regions of the Southwest, where ranges are so sparse as to make the production of

milk-fat lambs almost impossible, lambs usually sell as feeders at lighter weights and lower prices than those at which milk-fat lambs sell in areas where their production is possible. High-quality fine wool can be produced under these conditions. Thus, wool is relatively a much more important product than in better range areas or under farming conditions such as prevail in the Midwest.

Regardless of the relative emphasis given to wool and lamb production, the general objectives of sheep breeders are very similar, namely, to produce as many pounds of lamb as possible per 100 lb. of ewe and as much high-quality wool as possible. They must pay attention to prolificacy, ease of lambing, milking ability, and natural fleshing. As with dual-purpose cattle, some of these qualities are more or less antithetical. If he gets too great propensities for wool production and milking ability, natural fleshing is apt to suffer, and vice versa. In addition he must pay attention to general vigor and longevity, since susceptibility to diseases, parasites, or too rapid turnover of the flock all reduce immediate profit and lessen the effectiveness of selection.

As if all these things were not enough to worry about in a breeding program, the sheep industry is plagued with a greater diversity of breed trade-marks than is the case with other classes of farm animals. As pointed out earlier, some of these, such as excessive face covering, are actually detrimental to productivity. The modern breeder might be well advised to place emphasis on production records rather than winning show-ring type.

The largest and most highly organized project devoted to sheep-breeding research in the United States is the Western Sheep Breeding Laboratory established at Dubois, Idaho, in 1937. It has operated since that time under the guidance of Director J. E. Nordby. It is utilizing the facilities developed by the Bureau of Animal Industry Sheep Experiment Station, which was organized at Dubois in 1917, and in addition the experiment stations of the 11 Western states and Texas are cooperating.[1]

The main objective of the program is the improvement of sheep through breeding. The improvement is measured by the application of utility standards as they concern commercial production under ranching conditions. Production is measured on the basis of wool yield, and in pounds of lamb of the desirable type and finish. Obviously, the staple length and the quality and uniformity of fibers, as well as the shrinkage, are important factors that are studied with the yield of wool. All useful type characteristics that influence lamb production, ranch adaptability, and general serviceability are closely integrated in the improvement program. Under ranching conditions at relatively high altitudes, where winter

[1] From mimeographed statement on the Western Sheep Breeding Laboratory and the U.S. Sheep Experiment Station by Julius E. Nordby.

storms are frequently severe, the objectives in sheep improvement must also include a consideration of those characteristics in a fleece that protect the sheep against weather extremes. The fleece must be relatively long and "lofty" as well as dense and must hold together along the topline and cover well the underline.

Attention in selection is being given to both meat and wool production but with meat qualities[1] emphasized somewhat more than those relating to wool.

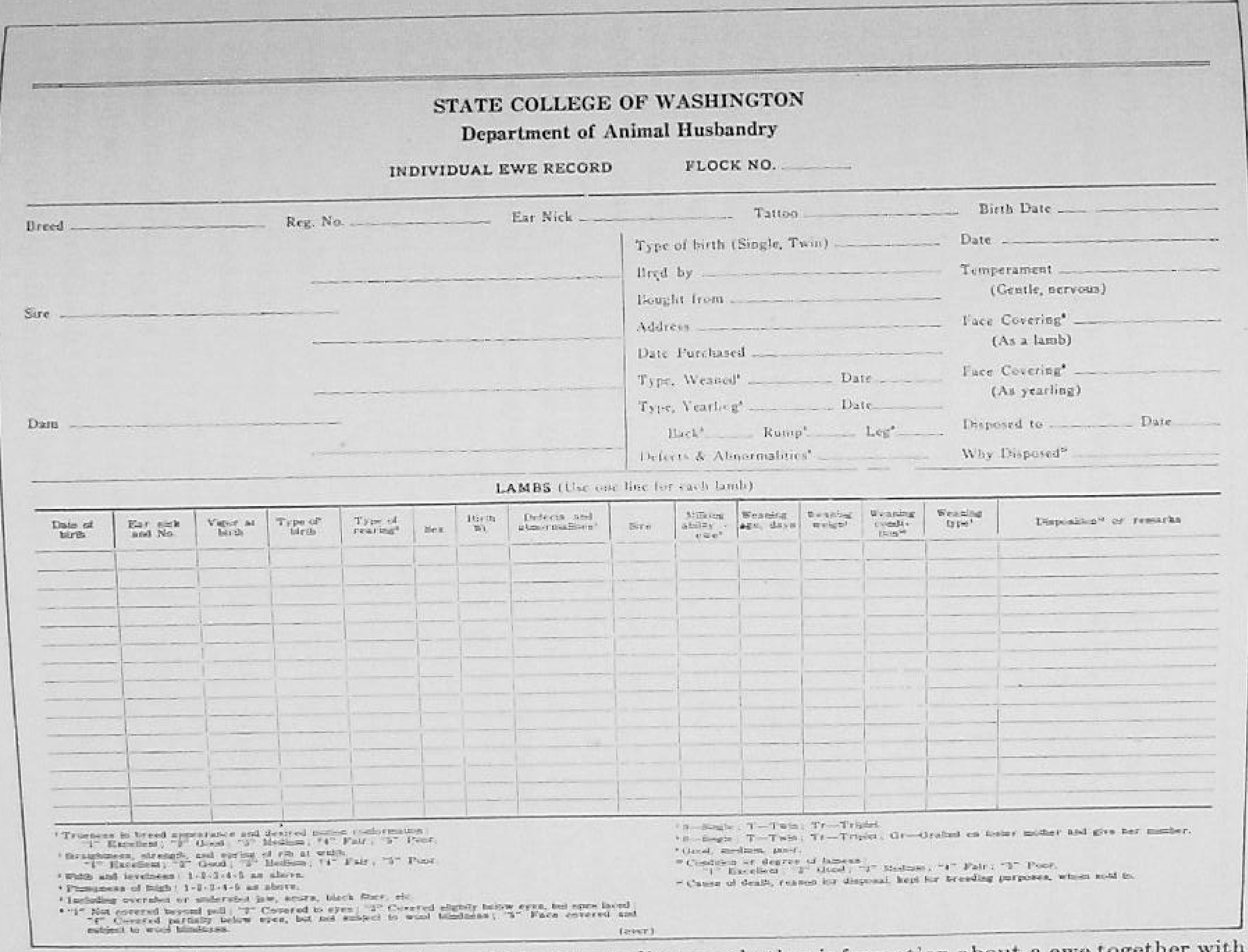
Besides we are interested in the mature form of mutton sheep on the basis of its value for producing the right kind of market and feeder lambs, and replacement ewes. While obviously the mature size, form, and fleshing quality of a sheep are important, the ranchman is perhaps fully as concerned with weight, form, and fleshing qualities at the time of weaning the lamb, because it is at this time that weight and form, but principally fleshing will determine if the lamb is a market lamb or a feeder lamb. The milking quality in ewes is observed just after lambing, and this is further checked in their ability to produce vigorous and fleshy lambs. In the selection program, therefore, much emphasis is placed upon the finish in lambs at the time of weaning. Due consideration is given to twins in this connection. Stud ram prospects are scored carefully for market qualities at weaning, because a ram lamb that has the acceptable growth, ruggedness, form and finish at weaning time is probably more apt to be a potential sire of lambs of the same kind, than is a more slowly maturing ram that does not develop these qualities before he is more mature. Vigor is an essential quality in the selection of ranch sheep. Some ewes, and rams also, "wear" uniformly well under heavy service until they are seven or even eight years of age. Others begin to decline early in life and are on the "cull" list at five or before.

Selection is being practiced against too heavy face covering that might lead to "wool blindness" and also against heavy skin folds.

Work is being done with the Rambouillet, Columbia, and Targhee breeds, with a few other breeds being used in certain studies and in test crosses. Inbreeding is being done with about 30 Rambouillet lines and 8 to 10 lines of each of the other two breeds being in process of formation. Noninbred control stocks in which the same type of selection is practiced as in the inbreds are also being carried to see whether the greatest progress can be made with or without inbreeding.

Many publications on factors associated with productivity in sheep, methods of evaluating breeding animals, heritability of various traits, and other things about which information is needed in properly carrying out a research program in sheep breeding have already come from the laboratory. Many of these will be referred to later in this chapter.

[1] *Ibid.*



STATE COLLEGE OF WASHINGTON
Department of Animal Husbandry

INDIVIDUAL EWE RECORD FLOCK NO. ______

Breed ______ Reg. No. ______ Ear Nick ______ Tattoo ______ Birth Date ______

Sire ______

Dam ______

Type of birth (Single, Twin) ______ Date ______
Bred by ______ Temperament ______ (Gentle, nervous)
Bought from ______
Address ______ Face Covering ______ (As a lamb)
Date Purchased ______
Type, Weaned ______ Date ______ Face Covering ______ (As yearling)
Type, Yearling ______ Date ______
Back ______ Rump ______ Leg ______ Disposed to ______ Date ______
Defects & Abnormalities ______ Why Disposed ______

LAMBS (Use one line for each lamb)

Date of birth	Ear nick and No.	Vigor at birth	Type of birth	Type of rearing	Sex	Birth wt.	Defects and abnormalities	Sire	Milking ability - ewe	Weaning age, days	Weaning weight	Weaning condition	Weaning type	Disposition or remarks

Width and levelness: 1-2-3-4-5 as above.
Plumpness of thigh: 1-2-3-4-5 as above.
S—Single; T—Twin; Tr—Triplet.
Good, medium, poor.

(over)

FIG. 205.—Individual ewe record form which gives pedigree and other information about a ewe together with an easily visualized summary of her lamb production record. (*Courtesy of State College of Washington, Pullman, Wash.*)

WEIGHT RECORD OF EWE

Date	Age	Weight	Condition[1]	Remarks[2]

REMARKS

(For example: bad udder, poor mother, aborted, veterinary treatment and nature of ailment.)

Date:	Remarks:

FLEECE
(Use one line for each year)

Length Side[3]	Fineness[4]			Date of Shearing	Days Growth	Grease Weight	Per cent of Yield	Clean Wt.	Color of Skin	Purity[5]	Remarks About Fleece
	Shoulders	Side	Thigh								

1. Condition or degree of fatness: "1" Excellent; "2" Good; "3" Medium; "4" Fair; "5" Poor.
2. Factors affecting weight: e.g. just shorn, soon lamb, etc.
3. Length of staple, middle at side, to nearest 0.2 cm., just before shearing.
4. Numerical grade as determined by U.S.D.A. samples, just before shearing.
5. Kemp, black fibers, etc.

(over)

FIG. 206.—Reverse side of the sheet shown in Fig. 205. Records of body weights and fleece production are kept in forms which permit a rapid appraisal of a ewe. (*Courtesy of State College of Washington, Pullman, Wash.*)

Definite progress has been made in improving sheep, especially for some of the more highly heritable characters. Because of the relatively slow rate of reproduction in sheep, inbreeding advances more slowly than is the case with hogs.

The keeping of production records on sheep and their intelligent evaluation in making selections necessarily entail a considerable expenditure of time and effort. Due to the variety of types of sheep it is difficult to suggest procedures for taking and evaluating records which will be universally applicable. However, the following items have been included in one form or another in most record-of-performance precedures suggested to date:

1. *Prolificacy of ewes* (regularity of lambing and twin production). In some areas where grazing conditions are poor, twin lambs may be a disadvantage, but generally twin-producing ewes are more profitable.

2. *Birth weights of lambs.* This item is of no value in itself but is related to vigor at birth and to rate of gain after birth.

3. *Weaning weights of lambs.* Taken individually but also used to measure total lamb production of a ewe. This latter may be best expressed as pounds of lamb weaned per ewe (in areas where costs are largely on a per head basis) or as pounds of lamb weaned per 100 lb. of ewe (best in areas where costs are more related to actual amounts of feed eaten than to total numbers).

4. *Type and finish of lambs at weaning.* These important factors reflect market value to a large extent. Attempts to evaluate these items objectively by means of measurements have as yet met with little success. Although unsatisfactory at best, the most successful means of evaluating these characters has been through the use of scores based on subjective appraisals of merit.

5. *Fleece weight and quality.*

6. *Regular annual or semiannual weights of all breeding stock.*

The evaluation of performance records is greatly complicated by environmental factors. Some of these, such as the effects of sex, age of dam, type of birth (single or multiple), and age at weaning, can be measured and definitely taken into account.

If these things are not systematically evaluated, selection may be biased in favor of lambs having the most favorable conditions for growth. A study of the lambs born during a 14-year period (1921–1934) in the Hampshire, Shropshire, and Southdown flocks at the National Agricultural Research Center at Beltsville, Md., showed that their environmental factors had apparently influenced selection to an undue degree when selection of lambs began at about three months of age. In summa-

rizing this study[1] the authors recommend some practices which should minimize this tendency.

The results showed that type of birth, time of birth, and birth weight have influenced the selection of breeding animals. Single lambs have been preferred to twins, early lambs to late ones, and lambs that were heavy at birth to light lambs. With the exception of a portion of the effect of birth weight, the effects of these factors on selection are considered to be environmental in nature, and therefore, reduce the chances of selecting the genetically superior animals for breeding purposes. This weakness in the present method of selection can be at least partly overcome in one of the following ways:

1. When selections are made at weaning or a similar early age, the animals may be divided, first by sex and then into single and twin groups within sexes. These last two groups should then be divided according to time of birth. If the range in date of birth is 6 weeks, the lambs may be divided into two groups having a range of 3 weeks each. If lambing occurs over a longer period, more groups may be necessary. With the animals so divided, those in each group will be on a more comparable basis than if considered as a whole, and selections can be made within each group. This division does not take into consideration differences in birth weight, and if data on this point are available they may be kept at hand for use while making selections. Selections would, of course, be based on the characters in which the breeder is primarily interested, such as mutton form, fleece, and perhaps other factors such as pedigrees of the animals.

This method eliminates comparison of single lambs with twin lambs and of early lambs with late ones. Assuming that the proportion of individuals possessing superior germ plasm is equal in the groups of singles and twins and that there is a similar proportion in the early and late group in each type of birth, the chances of actually selecting these superior animals would be greater if this suggested system was followed.

2. Selection may be made at a standard age, such as 6 months, rather than on a certain date. Weights at this age could be adjusted for the effects of birth factors, and any advantage or disadvantage kept in mind when evaluating each animal. The weights of all animals could be adjusted to a standard basis, such as single males of a standard birth date and weight, for use in making such allowances for the effects of birth factors and sex. All animals reaching the standard age within a given week might be observed on one day during that week. By this method each individual is compared with an ideal at a standard age, with allowance for any unfavorable environment due to birth factors. The effect on selection would be similar to that of the first suggested method.

3. Selections might be postponed until an age when the effects of the birth factors on development discussed herein have disappeared. Little effect of type and time of birth and birth weight on development, as measured by weight, remains at 12 months. Retention of all animals to this age is not practical for the sheep breeder who must sell his discarded lambs when they reach market

[1] Phillips, R. W., and Dawson, W. M., Some Factors Affecting Survival, Growth, and Selection of Lambs, *U.S. Dept. Agr. Cir.* 538, 1940.

weight, but it may be a worthwhile procedure in experimental breeding, unless data taken at younger ages can be shown to be sufficiently representative of the animals' potential development.

Another application of the results of the study presented herein is in the comparing of groups of animals, such as the offspring of two or more rams in progeny testing. If the number of offspring from each of two rams is sufficiently large that practically equal numbers of singles and twins, lambs of heavy and light birth weights, and males and females are available, and if the time of birth of the lambs is comparable, then a comparison of the uncorrected weights of the two groups at a standard age would be valid. However, most young rams are tested on a small number of ewes. If the resulting small number of offspring of a ram are to be compared with those of another ram at an age when the effects of birth factors still persist, the figures given in this circular, or similar figures, can be used in making necessary adjustments. Adjustments for sex can be made in like manner. All animals might be adjusted to a basis of male singles with date of birth and birth weight constant.

Recent extensive studies at the Western Sheep Breeding Laboratory (Hazel and Terrill, 1945a, 1946b, and 1946d; Terrill, Sidwell, and Hazel, 1947, 1948a, and 1948b) have shown that under range conditions the effects of sex, type of birth and rearing, and age of dam have important

TABLE 54.—DIFFERENCES IN PERFORMANCE OF RANGE SHEEP DUE TO SOME ENVIRONMENTAL CONDITIONS

	Weaning characters		Yearling ewe characters		
	Body weight, lb.	Staple length, cm.	Body weight, lb.	Clean fleece weight, lb.	Staple length, cm.
Rambouillets					
Advantage of:					
Rams over ewes	8.3*	−0.48*			
Mature dam over 2-year-old dam	6.1*	0.19	2.6	0.17	0.12
Singles over twins	9.2*	0.05	6.0*	0.23*	0.30*
Columbias, Targhees, and Corriedales					
Advantage of:					
Rams over ewes	10.8*	−0.54*			
Mature dam over 2-year-old dam	8.7*	0.52*	4.16*	1.04†	0.46
Singles over twins	11.7*	0.02	7.12*	1.03†	0.12

* Signifies statistic is large enough to account for 2% or more of the total variation in that trait.
† Grease fleece weight.

effects on body weight at both weaning and yearling ages, on fleece characters, and on type and condition as evaluated by subjective scores. Age of lamb at weaning also had a significant effect upon weaning weight. The environmental factors were relatively unimportant in affecting scores for face covering or neck folds.

Table 54, prepared from data in the papers just mentioned, shows the magnitude of some of the differences observed. In general, the differences tend to become smaller with advancing age. The reader should recognize that these figures will not necessarily be applicable to other flocks under other environmental conditions.

In a large operation, the necessary data to arrive at figures such as the above can be collected and the records all corrected to a single standard, preferably by adding the appropriate number of pounds to the weights of lambs in the lower groups to adjust them to the level of the heavier group.

In actual practice similar results may be obtained by sorting lambs into groups according to sex, age of dam, type of birth, and age of lamb and selecting the same proportion from the various groups.

Heritability estimates of a number of traits in sheep as given in Table 55 indicate that fleece characters, face covering, and neck folds are, in general, more heritable than body weights, and that subjective scores of body type and condition are considerably less heritable.

In a breeding program the relative emphasis to be placed upon the various characters depends upon (1) the economic importance of the character, (2) its heritability, and (3) the level of performance already attained in the flock. The latter two factors are interrelated since average performance near either end of a scale of desirability will be indicative of an approach to genetic fixation with a resultant low heritability. Hazel and Terrill (1946c) point out a situation which illustrates this fact. Jones *et al.* (1944) found a heritability of 51 per cent for neck folds in a moderately wrinkled Rambouillet flock, Terrill and Hazel (1946c) obtained an estimate of 38 per cent in a less wrinkled Rambouillet flock, while in Columbia and Targhees with only a slight degree of wrinkling the apparent heritability was only 8 per cent.

In a breeding program intense selection should first be practiced for traits which are economically important and highly heritable. Progress should be rapid in this phase of the breeding program; and after desirable levels of performance have been attained for these characters, attention can be turned to other less heritable traits where progress can be expected to be slower, but nevertheless important once it is attained.

As with other classes of livestock, observation indicates that selection has been effective over the years in modifying type and productivity in

TABLE 55.—ESTIMATES OF HERITABILITY FOR VARIOUS CHARACTERS IN SHEEP

Character	Heritability, %	Method used to estimate heritability	Breed of animals used in studies	Reference
Birth weight	30	Paternal half sib	Hampshire	Chapman and Lush (1932)
	61	Av. of 2 methods*	Av. of 5 breeds	Nelson and VenKatachalam (1949)
Weaning weight	30	Av. of 2 methods*	Rambouillet	Hazel and Terrill (1945b)
	17	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
	33	Av. of 2 methods*	Av. of 5 breeds	Nelson and VenKatachalam (1949)
Weaning type score	13	Av. of 2 methods*	Rambouillet	Hazel and Terrill (1946a)
	7	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
Weaning condition score	4	Av. of 2 methods*	Rambouillet	Hazel and Terrill (1946a)
	21	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
Yearling body weight	40	Intrasire regression	Rambouillet	Terrill and Hazel (1943)
Yearling body score	12	Intrasire regression	Rambouillet	Terrill and Hazel (1943)
Staple length at weaning	40	Av. of 2 methods*	Rambouillet	Hazel and Terrill (1945b)
	43	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
Yearling clean fleece yield	38	Intrasire regression	Rambouillet	Terrill and Hazel (1943)
Face covering score	56	Av. of 2 methods*	Rambouillet	Terrill and Hazel (1946)
	46	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
Skin folds	51	Av. of 4 methods	Rambouillet	Jones *et al.* (1946)
Neck folds	39	Av. of 2 methods*	Rambouillet	Terrill and Hazel (1946)
	8	Av. of 2 methods*	Columbia, Corriedale, and Targhee	Hazel and Terrill (1946c)
Number of functional nipples	22	Intrasire regression	Grades of mixed breeding	Phillips *et al.* (1945)

* Paternal half-sib correlation and intrasire regression of offspring on dam.

sheep. Numerous examples, including the work of Neale (1946) in selecting for staple length in Rambouillets and the work of Warwick *et al.* (1949) in selecting for resistance to stomach worms, can be cited to show the possibilities.

Terrill (unpublished data) in a study of data from the Western Sheep Breeding Laboratory has compared the amount of progress actually made for several traits in Rambouillet sheep during the period 1940–1948 with the genetic progress expected. The latter is calculated by comparing the averages of the animals which later became parents born in

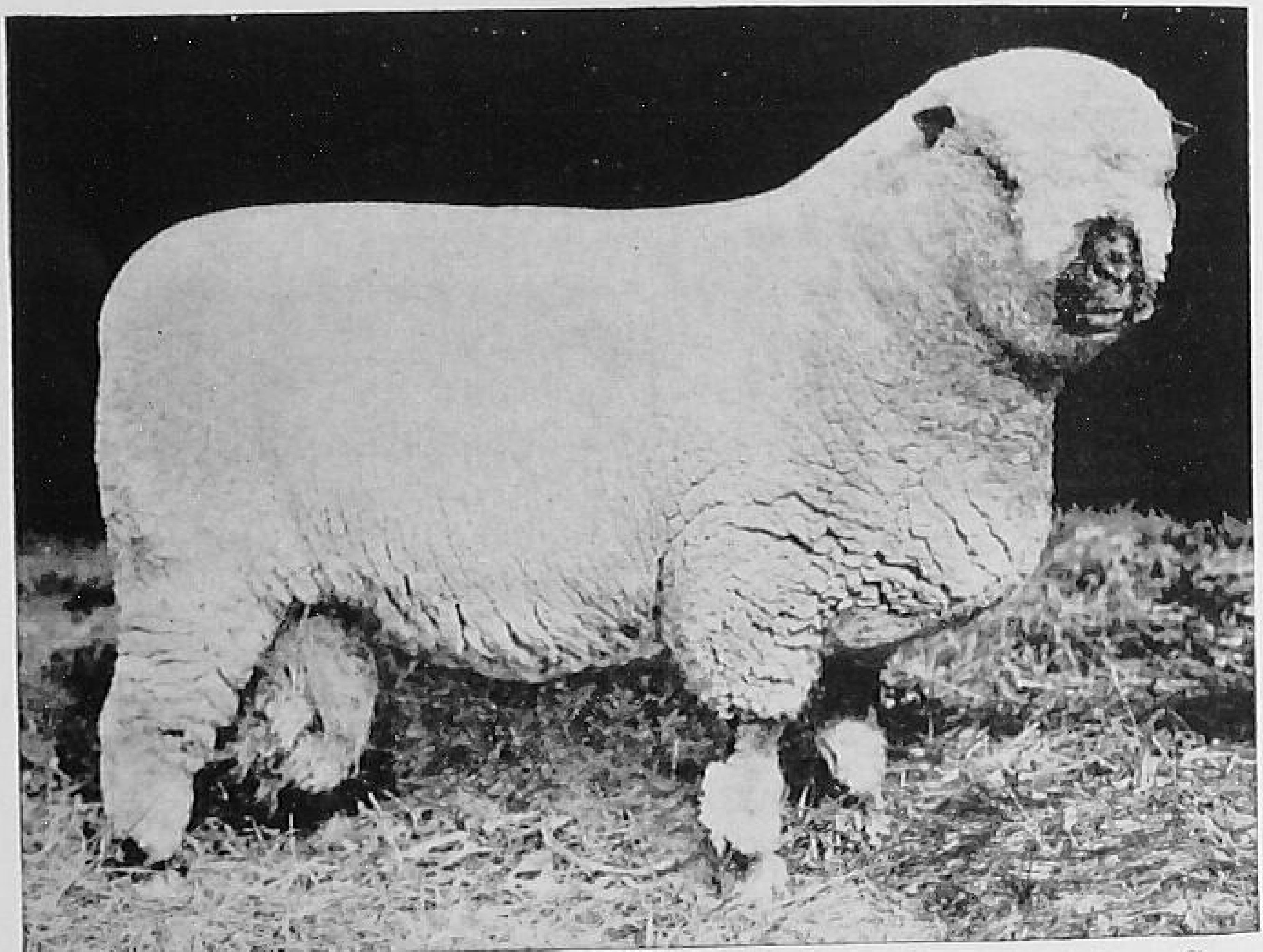


FIG. 207.—A model Shropshire ram, bred by George McKerrow and Sons Company, Pewaukee, Wis.

each year (suitably weighted for number of offspring produced) with the average of all sheep born in that year. These selection differentials were divided by the average age of parents and multiplied by the heritability of the trait being studied in order to give an estimate of expected annual genetic progress.

In evaluating his results, it must be kept in mind that trends in environmental conditions could have been responsible for some of the observed trends in productivity. Yearling fleece weights, weaning body weights, and weaning body scores for condition all trended slightly downward in average merit, in spite of positive selection for improvement. Improvement was shown in staple length, type scores, face-covering scores, and neck-fold scores. An index based on the above items, and thought to

reflect all-around merit, is used as the basis for selecting breeding animals in this flock. The average index has increased during the period of this study almost as much as would be expected, and Terrill concludes that the average merit of the sheep in the flock has improved.

Individual performance and family averages in production are the basic items upon which selection in sheep must be based. This follows from the facts that (1) although some culling of breeding animals may be practiced on the basis of the first lamb crop or two, they must initially be selected for use in a flock upon the basis of their own and relatives' performance, and (2) even if a progeny-testing program is followed with prospective stud rams before they are used in the main flock, only a small percentage of the most promising rams can be progeny-tested, these must be selected on the basis of individual and family performance.

An organized program in which prospective stud rams are progeny-tested in an auxiliary flock prior to being used in the main flock can be useful under certain conditions. Dickerson and Hazel (1944) concluded that a program of progeny-testing yearling rams and using the best ones in the main flock as two-year-olds or three-year-olds, should increase progress by about 20 per cent and 5 per cent for weanling and yearling traits, respectively, with characters having heritabilities as low as 10 per cent. For characters with heritabilities of 30 per cent, progeny testing would be expected to increase progress slightly for traits which could be measured at weaning age, but would be expected to decrease progress for those traits which could not be measured until yearling age. This latter situation occurs because of the additional year which it takes to evaluate yearling characters of the progeny.

Progeny testing can be expected to be still more effective if rams can be progeny-tested as lambs instead of yearlings and the best performing ones used in the main flock as yearlings.

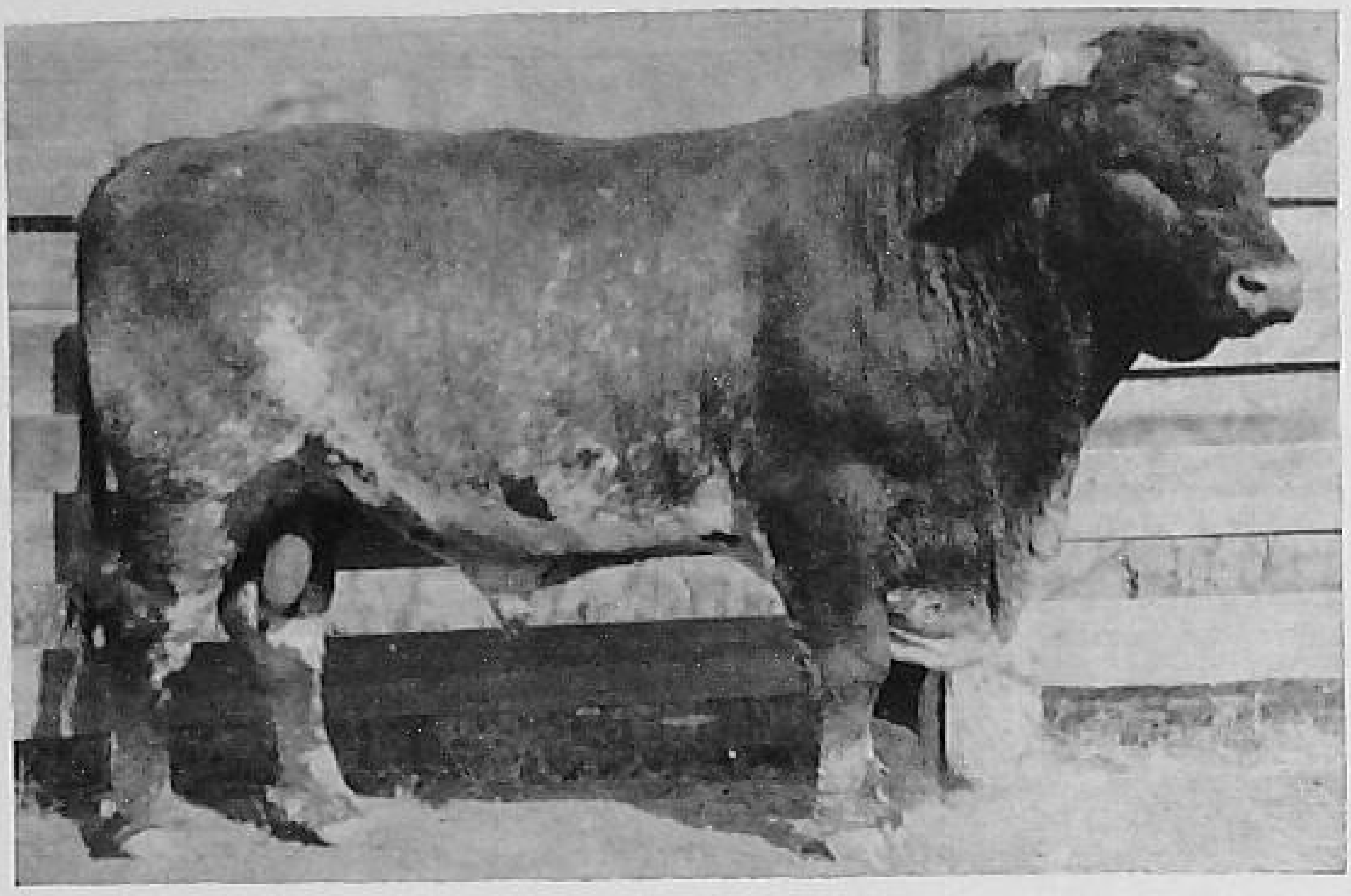
Selection in Beef Cattle.—Selection in beef cattle has long been based primarily upon show-ring winnings or type evaluations based upon show-

TABLE 56.—PERFORMANCE RECORD OF FOUR CHOICE BEEF SHORTHORN STEERS*

Steer number	Days on feed	Daily gain, pounds	Feed to produce 400 lb. of gain	
			Grain, pounds	Hay, pounds
1	239	1.71	1,930	864
2	225	1.77	2,251	926
3	306	1.35	2,796	1,174
4	287	1.38	2,809	1,768

* KNAPP, B. JR., *Ext. Anim. Husbandman*, June, 1940.

ring standards. The fact that the beef market tends to be a discriminating one makes it necessary to pay considerable attention to type in beef cattle, but much more information is needed regarding the relation between type and carcass quality.



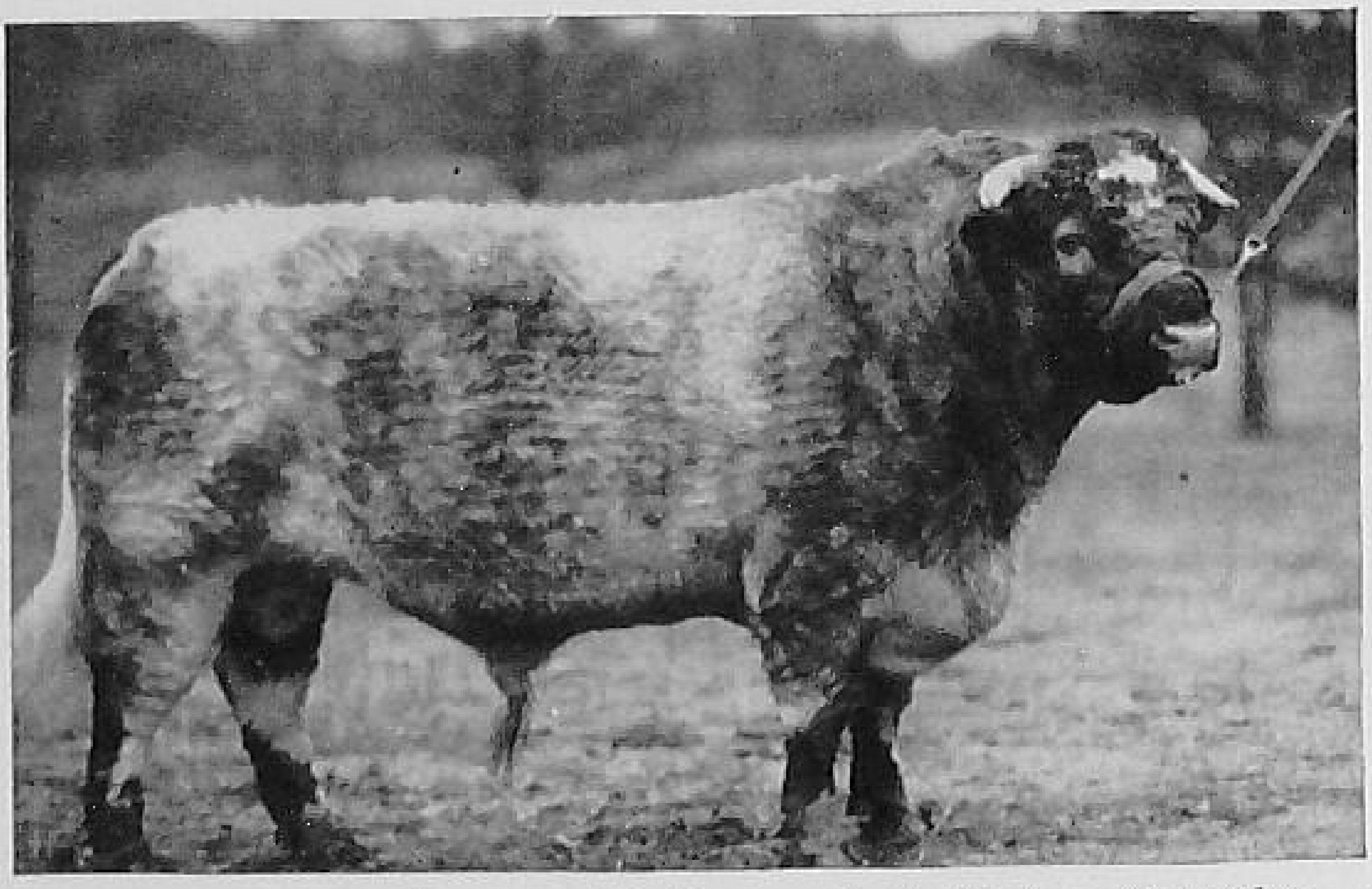


FIG. 208.—Appearance may not be a good indicator of a bull's breeding value. Calves sired by the bull at the top averaged 42 lb. heavier at the end of a feeding period and produced higher grading carcasses than calves sired by his more attractive half brother shown in the lower photo. (*Courtesy of Bureau of Animal Industry, U.S. Department of Agriculture.*)

Although all breeding work with farm animals is slow and expensive, such work with beef cattle is especially so because of slow reproductive rates. Much information has been accumulated during the past 15 to 20 years, however, which when widely applied promises to aid in the development of more profitable types of cattle.

Winters and McMahon (1933) in a series of experiments in which steers were fed individually, demonstrated rather wide differences between

individuals in gaining ability and in efficiency of feed utilization. Further extensive work by the U.S. Department of Agriculture has extended these observations (see Table 56 for some extreme cases), and it has been shown that sire progenies differ considerably in these same characters.

The few heritability studies thus far reported for beef cattle (Table 57) have almost all been from the same herd and seem to be unreasonably

TABLE 57.—HERITABILITY OF VARIOUS CHARACTERS IN BEEF CATTLE

Character	Heritability, %	Method used to estimate heritability	Reference
Birth weight	53	Paternal half-sib correlation	Knapp and Clark (1950)*
	11	Paternal half-sib correlation (corrected birth weights)	Dawson *et al.* (1947)
Weaning weight	28	Paternal half-sib correlation	Knapp and Clark (1950)
Live weight at 15 months	86	Paternal half-sib correlation	Knapp and Clark (1950)
	92	Sire offspring regression	Knapp and Clark (1950)
Gain during feeding period	65	Paternal half-sib correlation	Knapp and Clark (1950)
Rate of gain in feed lot	77	Sire offspring regression	Knapp and Clark (1950)
Score at weaning	28	Paternal half-sib correlation	Knapp and Clark (1950)
	0	Sire offspring regression	Knapp and Nordskog (1946b)
Slaughter grade	45	Paternal half-sib correlation	Knapp and Clark (1950)
Carcass grade	33	Paternal half-sib correlation	Knapp and Clark (1950)
Area of eye muscle	68	Paternal half-sib correlation	Knapp and Clark (1950)

* KNAPP, BRADFORD, JR., and CLARK, R. T., Revised Estimates of Heritability of Economic Characters in Beef Cattle (unpublished manuscript). This paper represents an extension of studies previously reported by Knapp and Nordskog (1946a and 1946b) but includes about four times as much material.

high for those characters reflecting feed-lot efficiency and carcass quality. However, even if further studies should indicate that the figures upon which these estimates are based were not typical of beef cattle in general and that the estimates need to be revised downward, it does appear likely that heritabilities are high enough for selection to be effective in bringing about improvement in these characters.

Several record-of-performance procedures have been proposed for beef cattle (Winters and McMahon, 1933; Sheets, 1932; Winters, 1940; and Bureau of Animal Industry, 1941), and the factors usually considered important will be listed and discussed briefly.

1. *Birth Weight.*—Although no one would advocate breeding beef cattle for extremely heavy birth weights, it has been shown that, within the normal weight range, heavier calves at birth tend to grow more rapidly later (see Dawson *et al.* 1947). Thus, birth weights are a desirable but not indispensable item in performance records.

2. *Weaning Weight.*—Weaning weight is important to all beef cattlemen because, in general, gains made prior to weaning are cheaper than those made later. The producers of calves for slaughter at weaning or of feeder calves are especially interested in heavy weaning weights because their income depends upon weight available for sale at that time. It has been assumed that growth rate from birth to weaning is largely a function of milk production of the dam. Gifford (1949) found gross correlations of +0.60, +0.71, +0.52, and +0.35 between daily milk production of 57 Hereford cows and daily gain in weight of their calves during the first, second, third, and fourth months, respectively. After the fourth month there was no significant relationship between the two items. From this data it would appear that, while milk production exerts an influence on calf growth, it is by no means the only factor involved.

It has long been assumed by animal husbandmen that heavier weaning weights are associated with rapid gains during a subsequent fattening period. Knapp *et al.* (1941), however, found virtually no correlation between these items. They also found that weaning weight was negatively correlated with efficiency of gain during a subsequent fattening period. Since the heavy calf at weaning gains as rapidly after weaning as a lighter one, he will reach a given market weight in fewer days because of his headstart. In all probability the lower efficiency of the heavier weaning calves is due to the fact that they have reached a more expensive part of the growth curve, and not to an inherently lower efficiency. Thus, these observations do not constitute an argument for selecting light weaning calves.

3. *Gain and Efficiency of Feed Utilization during a Feeding Period.*—Beef cattle are ordinarily fed a heavy grain feed for a period of time prior to

being marketed. The animal which gains rapidly during this period has to be fed fewer days, with a resulting saving in labor and a more rapid turnover of capital. The rapid-gaining animal also tends to be the most efficient. This relation is by no means absolute, however.

Since no other characters seem to be highly enough related to feed-lot performance to be of predictive value, feeding tests are needed to measure this important character. How such feed tests should be conducted is not a settled question.

Earliest proposals were for a feeding period of a fixed number of days after weaning. This is by far the most convenient method, but has the disadvantage that the animals may be in very different portions of the growth curve during the period of similar chronological age. In general, the heavy weaning calf will be at a disadvantage in efficiency evaluations because he will be heavier throughout the feeding trial and therefore in a more expensive part of the growth period. This method is, therefore, not well suited for measurement of efficiency (see Knapp and Baker, 1944), but since there is little or no relationship between weaning weight and subsequent rate of gain, it does provide a convenient and acceptable method of evaluating rate of gain for use in selection.

It was later proposed (Black and Knapp, 1938) that animals on test be fed through a given weight range, the suggested period being from 500 to 900 lb. live weight. They showed a very high relationship between rate and economy of gain using this method.

Guilbert and Gregory (1944) pointed out that animals differing in rate of maturity may differ greatly in composition at a given weight. Since the energy required to produce fat is greater than that required to produce lean meat and bone, it is apparent that the early maturing, rapidly fattening calf would be at a disadvantage in evaluating efficiency. They recommend feeding to a definite degree of finish in an effort to control the composition of the gains.

Although there is no basic relationship between size and efficiency, many of the overhead costs of livestock production tend to be on a "per head" basis. Thus, as Brody (1939) has pointed out, it may be more economical to produce the same amount of product from fewer animals of large size than from a larger number of smaller animals.

It would appear, therefore, that the method of selecting on the basis of rate and economy of gain during a constant weight period would be satisfactory from a practical standpoint *if* it were combined with selection for satisfactory carcass finish at the desired weight.

All investigators are agreed that the feeding period should be one of full- or self-feeding. Knapp and Baker (1943) found that genetic differences were not expressed between sire progenies if a limited feed

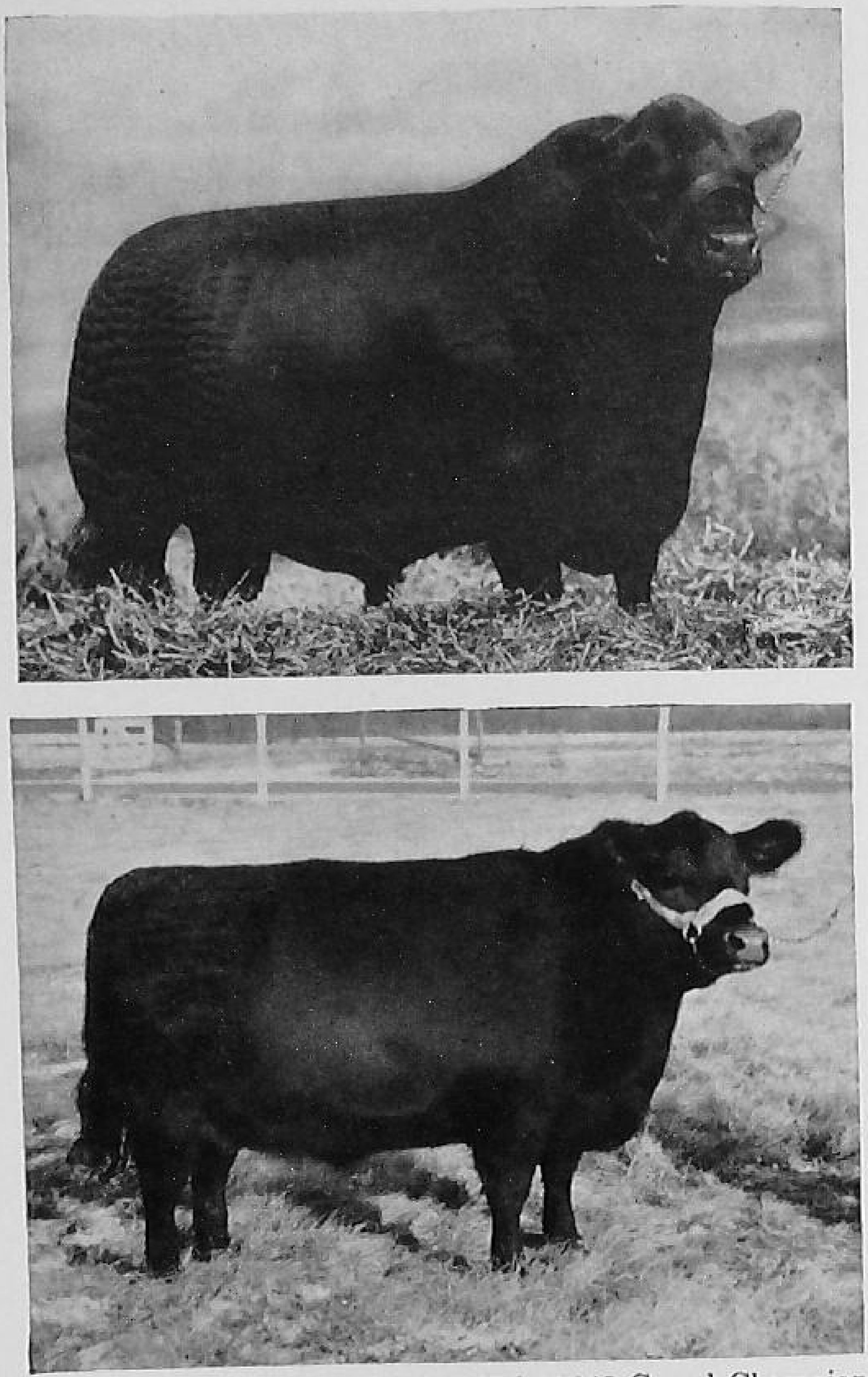


FIG. 209.—Angus bull (*top*) Prince Sunbeam 249th, 1948 Grand Champion bull at International Livestock Show, shown by Ellerslie, Charlottesville, Va.; and cow (*bottom*) Eileenmere's Effie W., Grand Champion female, 1948 International Livestock Show, shown by J. Garrett Tolan Farms, Pleasant Plains, Ill. (*Courtesy of American Aberdeen Angus Breeders' Association.*)

intake put a ceiling on rate of gain. Knapp and Clark (1947) found that genetic differences in rate of gain were not fully expressed until late in a long feeding period. The apparent heritabilities of gain were 10, 54, and 84 per cent in the first, second, and third 84-day periods of a 252-day feeding period, respectively. Thus, the chance of getting very much genetic information from a feeding period of less than 168 days appears to be slight.

4. *Type and Carcass Evaluation.*—Type in the live animal can be best expressed in terms of a grade or score given to each animal at the end of the feeding period. For the steer progenies slaughtered, carcass grades should be taken as the best possible evaluation of type.

The above discussion points out the records which are valuable in beef production. Although the most efficient method of using performance records in selection cannot be stated with certainty, it does appear that each breeder can work out a system which, although it may not be perfect, will be distinctly superior to no records.

Each calf should be evaluated on the basis of his own birth weight, weaning weight, rate of gain, efficiency of gain, and body type.

A dam should be evaluated on the basis of her calves' performance, with special emphasis on weaning weight since it reflects maternal ability. More than one record is desirable for evaluating a cow, since the correlation between the weaning weights of calves from the same cow is only about +0.50 and between type grades only +0.33 (Koger and Knox, 1947). Koger and Knox found, however, that a heifer whose first calf was decidedly poor (barring accidents such as crippling) was never a heavy producer later in life. Thus, some culling of first-calf heifers can be safely done with little or no chance of discarding a valuable cow.

Efficiency records on individual animals can only be obtained if individual feeding is practiced. This expensive practice is probably not practical for the average breeder. He can, however, group feed and get individual weight records, and if the groups are fed by sires can get sire-progeny efficiency records.

Theoretically, sires can best be evaluated upon the basis of the performance of a number of offspring, preferably at least eight to ten. Since rate and economy of gain are apparently relatively high in heritability, it may be that progeny testing is not needed for sire evaluation. The U.S. Department of Agriculture has recently been experimenting with the method of evaluating prospective herd bulls upon the basis of their performance under a heavy grain-feeding program for a period of 6½ months. Those animals performing best can then be used for breeding in the regular herd at about fifteen months of age without waiting the additional 2 years necessary for progeny-test information.

Results to date indicate a high correlation between the performance of a sire and that of his get. This is to be expected if heritability is high. This method needs extensive trial in other herds.

Full feeding of prospective breeding heifers is ordinarily not practiced, but many prospective show animals are full-fed without apparent harm. If heifers are to be properly evaluated for gaining ability, it is desirable

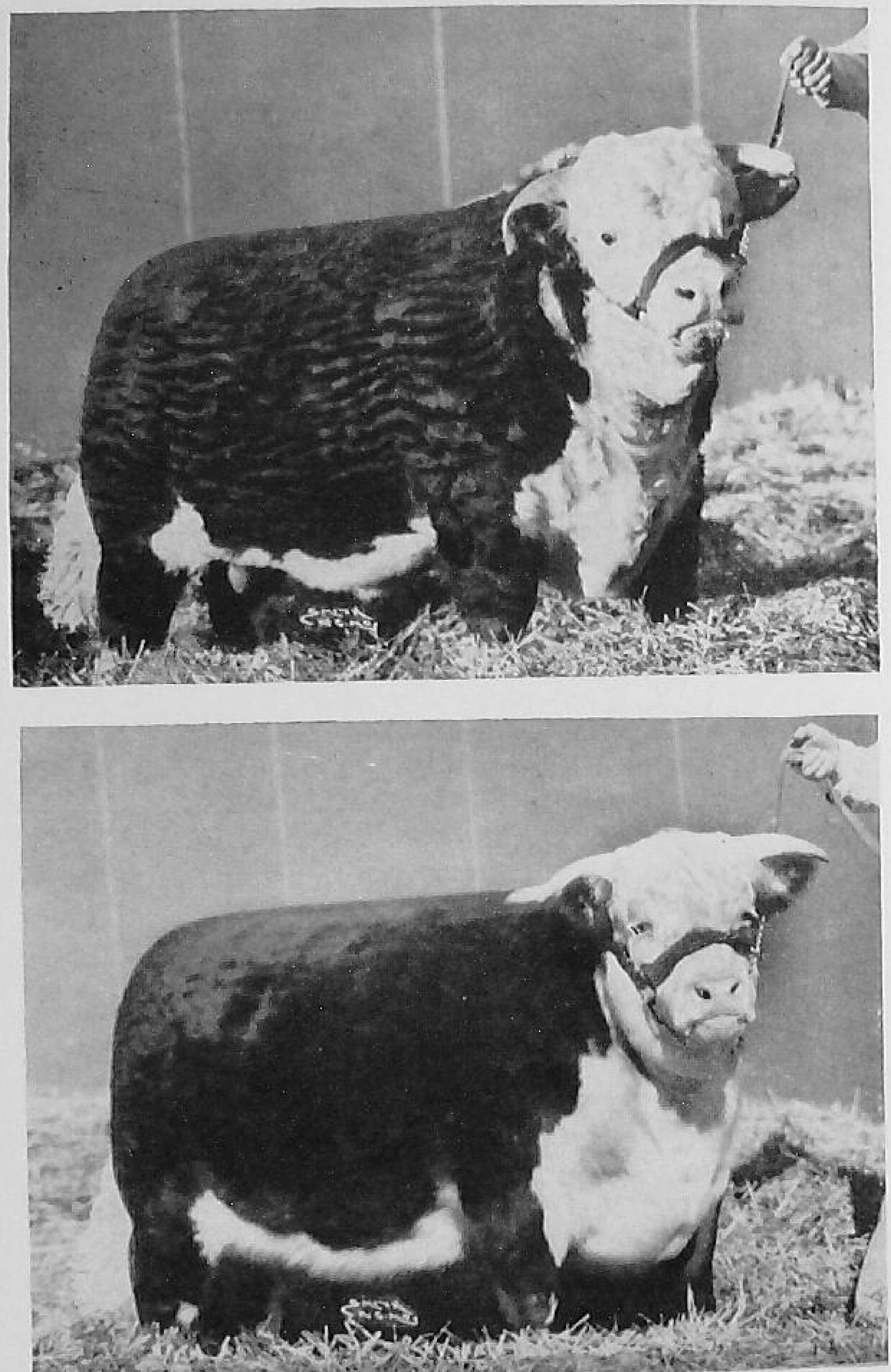


Fig. 210.—Hereford bull (*top*) MW Larry Mixer 1st, champion Hereford bull of the 1949 American Royal Livestock Show, Kansas City, Mo. Bred and shown by the Milky Way Hereford Ranch, Phoenix, Ariz.; and Hereford cow (*bottom*) JJ Gertrudis, reserve champion Hereford female of the 1949 American Royal Livestock Show, Kansas City, Mo. Bred and shown by Jack Haley, Escondido, Calif. (*Courtesy of American Hereford Association.*)

to full-feed them for a period, although it is recognized that this may not be possible in some cases.

A cooperative beef-cattle breeding program has been recently started by the U.S. Department of Agriculture and cooperating state experiment stations, with Dr. R. T. Clark of Denver, Colo., as coordinator. Inbreeding and performance testing are being carried on by a number of experiment stations. Due to the slow rate of reproduction in cattle, this program can not be expected to produce results so rapidly as the Regional Sheep and Swine Breeding Laboratories. The progress of this program will be watched with interest.

Fig. 211.—Lassie of W.T. 92607, Grand Champion Red Poll female at the 1949 Indiana State Fair. The Red Poll is a dual-purpose breed of cattle. (*Courtesy of Purdue University, Lafayette, Ind.*)

Selection in Dual-purpose Cattle.—Because dual-purpose cattle are kept both for milk and beef production, it is obvious that breeders should use both the index commonly in use in dairy herds as well as the one now in process of formation for beef animals. The problem here is similar to that found in all classes of livestock, *viz.*, the securing of sufficient data so that selection may be practiced in keeping with the known laws of inheritance, in other words that it rest on a sound genetic basis.

Dual-purpose cattle selection is not very different from that prevailing in all other classes of livestock, for most breeders try to select for more than one thing at a time. Here we are selecting for two major things at once, milk and beef, and in addition the two things are to some degree antagonistic. We know, therefore, at the start that we will probably never combine both things in their extreme degrees in any one animal. The beef breeds have many genes for beef production and a few for milk production owing to the breeding and selection that has been practiced

in the past. The opposite situation, of course, prevails in the dairy breeds. Dual-purpose cattle breeders want about a 50-50 combination of beef and milk genes. Discovering the animals that come closest to having such a genetic make-up by testing and record keeping, followed by intelligent mating and the use of some degree of inbreeding, should eventually produce superior strains of dual-purpose animals.

Summary.—In this chapter we have reviewed the evidence that hereditary differences exist in virtually all characters importantly related to the efficient production of high-quality meat-animal products. It has been pointed out that there is a definite relation between visual appraisals of type and carcass quality of enough importance that individual appearance will continue to be used as one criterion of quality. Visual type appraisals are, however, poor indicators of productive efficiency and must therefore be supplemented with production records if maximum progress is to be made. The breeding of meat animals is just beginning to be treated as a science, and we can look forward to an increasing rate of development in the future.

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CHAPTER XXIII

SELECTION IN HORSES

The creation by selection of the various types of horses from one or a few wild progenitors has been one of man's most interesting and most helpful accomplishments. The development of more efficient power to accomplish physical labor is simply the story of an advancing civilization. As a savage, man's only source of power was his own muscle, and in order to survive he had to use it so continuously that little time or energy was left for cerebration. At some time the idea dawned of using animal power to supplement or replace his own limited supply, and many animals have been so used, among others the dog, ox, yak, camel, llama, goat, elephant, ass, and horse. Later, water, steam, gas, electricity, and gasoline were used, and now the tremendous power of the atom is about to be harnessed for constructive progress.

The following figures[1] suggest the very rapid rate of increase in mechanical power in the United States.

Year	Total horsepower in prime movers	Horsepower per capita
1860	15,793,000	0.50
1900	64,193,000	0.90
1940	1,230,816,000*	9.35

* For tractors and automobiles drawbar equivalent was used rather than rated horsepower.

If we calculate that 1 horsepower is the equivalent of 10 man power, it is evident that each person living in the United States in 1940 had as his servants the equivalent of about 93 slaves. (Like the writer, you probably wish at times that some of these 93 were a little nearer at hand.)

Savages existed with no source of power save their own muscle, and without the adoption of outside sources of power we would still be eking out a precarious existence as savages.

In 1787, the year the Constitution was framed, the surplus food produced by 19 farmers went to feed 1 city person. In recent years 19

[1] Figures supplied through kindness of Z. R. Pettit, chief statistician for Agriculture, Bureau of the Census, Department of Commerce, Washington, D.C.

people on farms have produced enough food for 56 nonfarm people plus 10 living abroad.[1]

This is probably due, for the most part, to the fact that the modern farmer has more efficient sources of power. In ancient times a few people could live well and enjoy leisure because they had enslaved other human beings who were compelled to work for their keep. Today our slaves in America are machines.

Among the animals that have been domesticated and whose energy has been used to supplant human muscle, the horse is the most interesting and the most important. Next to the dog, among the larger animals, the horse apparently has the greatest capacity for responding to man's friendship. From the earliest times he was both helpmate and companion. The maximum efficiency of both man and horse during work, according to the researches of Brody and Trowbridge,[2] stands at 24 per cent, with steam engines at 15 per cent, gasoline engines at 18 per cent "at the belt" and about 13 per cent "at the drawbar," and Diesel engines at 35 per cent. Many other factors, of course, are involved in the choice of the "best" source of farm power.

In addition to supplying power, the horse had filled a great variety of human needs. History, unfortunately, is too largely the story of war and conquest, and, although "struggle" is the keynote and first necessity of a nation's or an individual's progress, it is to be hoped that less devastating forms of struggle than war can speedily be devised. Associated with the famous warriors of the past, there generally is found their favorite horses, *e.g.*, Alexander the Great and Bucephalus, Napoleon and Marengo, Washington and Nelson, Grant and Jack, Lee and Traveler. These men's names live in history; their physical likenesses, generally astride their favorite horse, on canvas or in bronze. The place of cavalry in war is too well known to need repetition here, and the same is true of the place of the horse in moving supplies, guns, and other equipment. During the First World War the United States shipped abroad for war purposes nearly 1 million horses and over ⅓ million mules. And, in spite of motorization, the horse played an important part in the Second World War, for Germany is estimated to have used over 200,000 horses and mules in the Polish campaign and 750,000 in the conquest of the Low Countries and France.

In addition to his services in work or war the horse has filled, and will

[1] McCrory, S. H., Hendrickson, R. F., and Committee, Technological Trends in Relation to Agriculture, reprint from Report of Subcommittee on Technology to the National Resources Committee, 1937, p. 99.

[2] Brody, S., and Trowbridge, E. A., Efficiency of Horses, Men, and Motors, *Mo. Agr. Expt. Sta. Bul.* 383.

probably continue to fill, a great place in pleasure and sport. In colonial America, he provided the most rapid means of land transportation. The American Standardbred and Saddlebred finally grew out of this in the Southern colonies, and even today Virginia, Tennessee, and Kentucky retain first place in the production of this light-horse type. The Middle and Northern colonies developed a somewhat heavier general-utility horse, which provided the basis for the later draft-horse development. Riding, racing, and polo still claim the attention of millions of Americans, and there appears to be little likelihood of abatement of this interest.

As a source of power in cities and on farms the horse is having serious competition from the gasoline engine. Both the motor and the horse have advantages, some of which are listed below:

Motor Advantages	Horse Advantages
More work in given time	Lower initial investment and depreciation
No permanent unsoundnesses or disease	Power of reproducing
Can work day and night	Live on home-produced feeds
No care nor fuel while not working	Flexibility-use 1 or 30
Less man power needed	Help maintain soil fertility
Use for belt power and custom work	Less actual cash outlay

The advantages of one are to a certain if not the full degree disadvantages of the other. Whether motors will entirely displace horses as a source of farm power is for the future to answer. The American farmer, like workers in all other fields, is becoming more and more efficient, *i.e.*, he produces more in less time and with less human physical effort. This tends to create a puzzling economic problem, for it means we cannot profitably consume all that is produced if all work as many hours a day or a week as they did under less efficient methods of production. As individuals, we are not interested in efficiency for efficiency's sake but only in translating efficiency into better living for ourselves and our families. If our efficiency can be made to mean a greater net income or the same income from less hours of labor, the average man is definitely interested. Hours of labor have shown a steady decline for the past 40 years; it is probable that the bottom in decreased labor time has not yet been reached.

The farmer is on the lookout for more efficient sources of power. If engineers can provide machines that can do the general run of farm work more efficiently and more cheaply than can the horse, it seems certain that farmers will find ways to buy these machines. Table 58 shows something of the trend in forms of power on the farm.

TABLE 58.—POWER ON FARMS

	1920	1930	1940	1945
Horses and mules	25,742,000	19,124,000	13,931,000	8,274,000
Tractors	229,332	920,021	1,567,430	2,458,628
Farms with electricity	....	841,310	2,032,316	2,787,624
Trucks	150,000*	900,385	1,047,084	1,490,300
Automobiles	2,000,000*	4,134,675	4,144,136	4,148,275

* Estimate.

In any event the farm horse is going to have to try to meet this competition. It seems unlikely that the farm horse will be totally replaced by machines, and it is evident that horse breeders must use every possible means to improve their methods of selection so that only sound, durable, and efficient types of horses will be produced.

Many farmers who keep horses and raise colts do not have sufficient numbers of animals to justify the keeping of a stallion, which means that they must patronize various and sundry owners of stallions. In the early part of the twentieth century, there were many unsound and poor-type stallions and jacks standing for public service at low service fees in the Midwest, and many also that were improperly registered. In order to protect both the owners of good purebred sires and the owners of mares, some states inaugurated stallion-enrollment or licensing services, which required the payment of a fee for enrollment or licensing, provided the stallion was adjudged sound upon inspection by a veterinarian, and the inclusion of a copy of the license in all advertising. Other states were, of course, forced to follow suit to prevent the dumping within their borders of inferior stallions from states that had adopted such legislation. This is the only class of animals in which legislation has been invoked as an aid in bringing about improvement. Twenty-two states from New York and New Jersey on the Atlantic to Washington and Oregon on the Pacific and including New Mexico and Oklahoma in the South now have stallion registration boards, and a national association of these state boards was formed in 1910 and is still functioning with Prof. W. L. Blizzard of Oklahoma as its president and Prof. R. B. Cooley of Indiana as secretary.

Although the state laws for licensing stallions and jacks vary somewhat, in general it may be said that to be eligible for public service a stallion must be free from sidebone, ringbone, bone spavin, curb (when accompanied by curby formation of the hock), glanders—farcy, *maladie-du-coït*, urethral gleet, and mange. He must be registered in a nationally recognized registry association or be advertised as a grade. In some

states only sound purebred stallions are eligible for a license. In other states an unsound stallion or jack may be licensed, but the nature of the unsoundness must be shown on the face of the license.

The main purposes of stallion-enrollment laws were and are to prevent misrepresentation in advertising and to prohibit the use of sires thought likely to spread infectious diseases or a conformation that would not stand up under hard work and, conversely, to encourage the development of a sound breeding program for horses. That these stallion-enrollment laws have accomplished their main purposes cannot be questioned, and, although it is impossible to estimate their financial advantages to breeders, farmers, and the respective states, their contribution to a better average type of horse is admittedly very great.

General Bases for Selection in Horses.—In general there are five types of horses, *viz.*, draft, heavy harness, light harness, saddlers, and ponies. They are maintained in the final analysis for but one thing, their ability to move for its own sake, as in the various types of racing, driving, hunting, riding, polo-playing, etc., or their ability to move loads, as in various forms of draft work. The criterion of selection in horses has always been their ability to do certain things plus, in some instances, their beauty of appearance. In the heavy and light harness horses, the pony, and the Saddle Horse used in the show ring, perhaps equal weight has been given to appearance and performance. In the hunter, utility saddler, draft, and various types of racehorses the main influence shaping selection has been performance, with somewhat less attention paid to appearance. The distinct types of horses have evolved quite naturally, as breeders selected those which excelled in the various types of performances, and so it has come about that in horses perhaps more than in any other class of livestock "type is production." Draft power calls for a compact, heavy, low-set, heavily muscled, and clean-boned animal with a relatively docile disposition. Speed calls for a lithe, lean, relatively long-muscled and light-boned animal with plenty of animation and a highly developed nervous temperment. The individuality of the animal, its phenotype, because this so closely correlates with its performance, is and should be the most important consideration in selection.

Pedigrees, if relatively complete in terms of records of performance (work, speed, show winnings, etc.), can be of very great usefulness in providing a safer basis for selection; and progeny performance, as in all classes of livestock, provides the one unassailable test of an animal's breeding merit. Performance records are available for various types of racing horses, which provides something comparable to milk-production records in cattle. To a limited extent, show winnings are available for heavy and light harness horses and Saddle horses. The dynamometer

is available for the testing of draft power in heavy horses, but thus far it has not been used in any practical way to help in the selection of draft horses.

The principles of inheritance in horses are similar to those in all other classes of livestock. The horse is the product of its genes times its environment. In this class of livestock, the environment in the form of training plays a much more important part than is true in any other class of livestock. Proper feeding is essential if any animal of any class is to grow out to the normal set by its particular genes. Cattle, sheep, and swine require no particular training, whereas training in the horse is fully as important as good genes. An offspring of Dan Patch and Lou Dillon would hardly be expected to do 1 mile in 2 minutes if it had grown up on pasture and spent the years from three to five pulling a grocery or laundry wagon.

More also in horses than in other classes of livestock do we need balance between the several parts of the body and between the physical and the mental make-up. We can overdo compactness in a draft horse until we reach the point where we have an animal that cannot move effectively. We want length of leg in a racehorse, but we can reach the point where further increase in length of leg detracts from rather than adds to speed. Likewise, we can have too phlegmatic a draft horse or too high-strung and nervous a Thoroughbred.

The halving and sampling nature of inheritance prevails in the horse as well as complex interactions between groups of genes providing favorable and unfavorable "nicks." We still have far too many horses ill-adapted, both from a genetic and from a training standpoint, for the purpose they are supposed to fill. With the number of horses declining, it is of great importance that we use all means available, and perhaps design new ones, to measure both the performance and the transmitting qualities of those remaining, so that the less efficient may be the first to go and the better genes discovered and put together in more desirable and homozygous combinations.

Buying Horses.—Buying a horse, even for the initiated, is something of a gamble. This is due to the fact that, in the short space of minutes or hours with the knowledge that many faults can be temporarily covered up through clever manipulation, we must evaluate a complex physical and mental make-up for use over long hours of work through days stretching into years.

As with all other classes of livestock, the first consideration is that of general health. Horses that have been shipped or have passed through sales stables may have had the opportunity of picking up various germs such as those causing pleuropneumonia (shipping fever) or influenza.

Such ailments very seldom prove fatal, but, if carried home to a group of horses, considerable inconvenience may be caused.

Since the horse is maintained for his ability to transform energy into useful work or to provide pleasure and companionability, one of the most important things to be appraised is his disposition. Whether or not there are genes for obnoxious dispositions in animals or man is not known, but something does occasionally give rise to bad dispositions, and whether genetically or, probably more often, environmentally caused, we do not want them. Undesirable dispositions may manifest themselves in the stall as halter pulling, kicking, biting, crowding, stall walking or trotting, weaving, cribbing, wind sucking, manger chewing, tail rubbing, etc., and outside the stall as an unwillingness to be harnessed, balking, running away, stumbling, etc. Work becomes doubly hard when it must be performed with the aid of recalcitrant beasts, and in a horse maintained for purposes of pleasure the first prerequisite is good manners. Even if not dangerous or particularly obnoxious, many of these faults and vices consume considerable energy for which the owner gets no return.

In addition to securing healthy horses that are free from objectionable manners and vices, one must, of course, select horses whose types fit them for the specific functions that they are intended to fulfill. This, of course, has many gradations from ponies to draft horses. Limitations of space and the general availability of excellent discussions on types of horses for specific requirements in book and bulletin form make both impossible and unnecessary similar discussions at this point. Since the value of a horse depends so largely on his ability to move from place to place, his feet and legs should receive first and major attention or, said more concisely, "no foot, no horse." Fully as important, however, are the matters of sound wind and good eyes. Any unsoundnesses of feet or legs, inability to breath easily and normally, or any impairment of vision should be avoided in purchasing horses. Since he is not a gift horse, better look in his mouth too in order to check on the soundness of his teeth as well as his age.

One final consideration remains, after having checked on a horse's freedom from vices, his disposition, his soundness of foot and limb, wind, mouth, and eyesight, his action, his general type of build as to the work or service it is intended to have him perform, *viz.*, his adaptability for specific work.[1]

A horse may possess proper conformation, be sound, and have good action yet still not be well adapted for a specific work; consequently it is very essential that he be thoroughly examined at the work for which he is wanted. If the

[1] Reese, H. H., How to Select a Sound Horse, *U.S. Dept. Agr. Farmers' Bul.* 779, pp. 21–22.

horse is to be used for heavy hauling for draft purposes, steady pulling under all conditions is an indispensable quality. For harness use the horse should drive promptly and freely with an easy, rapid gait and an alert expression, taking just sufficient hold of the bit to be in hand without causing the driver to pull on the lines. The saddle horse should have an easy, prompt mouth, style, graceful carriage and should stand quietly to be mounted and dismounted.

Some horses are difficult to harness and object to taking the bit in their mouths; others jump when an attempt is made to place a saddle or harness on their backs; while still others offer a great deal of resistance to having the crupper placed under their tails, which, if due entirely to general muscular strength and tension, may be an indication of endurance. While being hitched up or mounted the horse should stand quietly and should start promptly but quietly on command. For any purpose the following vices should cause the animal to be rejected: balking, backing, rearing, kicking, striking with the forefeet, or running away. Less important vices are: throwing the head up or down, shying, scaring, breaking loose when tied, resting one foot upon the other, grasping the bit between the teeth, rolling with the harness on, or switching the tail over the lines. Occasionally the last named vice causes the horse to kick, in which case it becomes dangerous.

Enlargements or scars (due to deformity, unusual mishap, or uncommon disease) not conforming to any of those discussed should cause a horse to be rejected unless the nature of the cause and the detriment to the value and usefulness of the animal is self-evident.

Experience gained by examining large numbers of horses will aid in quickening the eye and judgment, thereby making it possible to perceive readily any unusual condition, but it should be remembered that a hurried examination is liable to prove a disappointment: consequently plenty of time should be taken in making the examination, because time is much cheaper than money tied up in an unsatisfactory horse. In some countries nine days are allowed by law to the purchaser in which to learn of the serious forms of unsoundness or vice in a horse, so that in this country it would seem fair to allow at least a day for a trial when practicable.

If possible, get a history of the animal, and while you are about it get a history of the person having it for sale. So many defects may be covered up by such unfair methods as drugging that it is a good plan to make purchases only from persons with good reputations.

Horses offered at auction sales should preferably be thoroughly examined previous to their being brought into the ring; at least they should be tried out in compliance with the rules of the sale before time for settlement.

Finally, it is well not to form the habit of seeing only the defects, for horses, like people, are seldom perfect; consequently in judging them weigh the good qualities against the bad. A horse should be valued by the amount of service it will perform rather than by its minor shortcomings.

In case of the purchase of mares intended to serve in whole or in part as brood mares, attention should be given to their pedigrees, their collateral relatives, and their offspring in addition to their own individuality.

Breeder Must Know His Own Band First.—In spite of the fact that horses by and large have been selected on the basis of a phenotype lending itself to the efficient performance of specific tasks for a considerable period of time, they are as yet far from homozygous for desirable genes. The best appearing mare may not beget the best-type foal when bred to stallion A although she might if bred to stallion B. It is a worth-while and sometimes very surprising exercise to lead out our animals by families, standing the foundation female at the head of each separate female line and arranging her offspring behind her so that all the offspring of each successive sire used will form a line at right angles to the female lines.

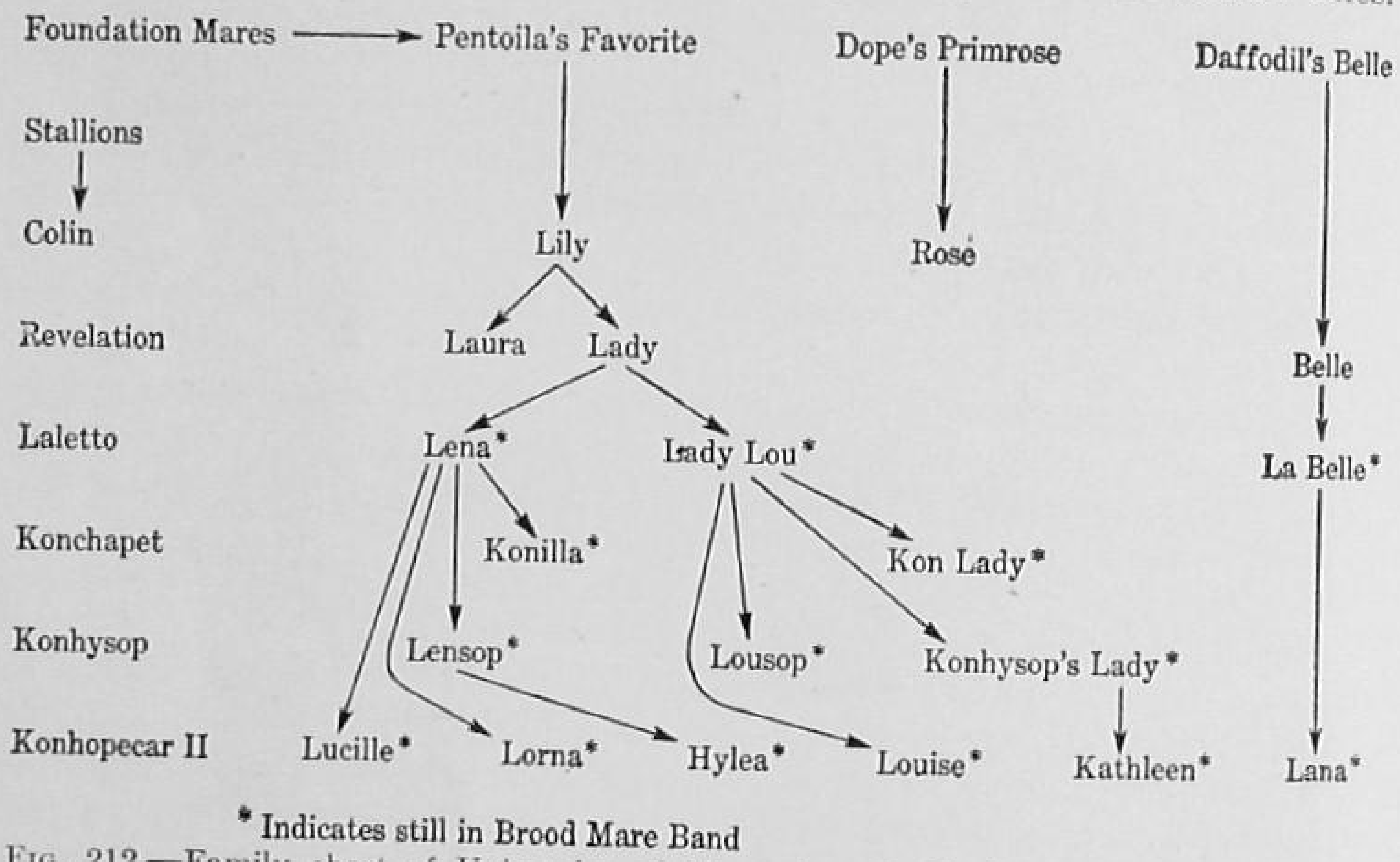

FIG. 212.—Family chart of University of Massachusetts Percherons. Only females in living lines shown.

This is easily done with horses and provides the opportunity for studying the whole band of mares with their offspring, of sizing up and evaluating the contributions of both sires and dams and arriving at an estimate of the good and bad features of the group as a whole, and of visualizing the trend which the group as a whole is apparently taking.

The story of the Percheron breeding at the Massachusetts State College is shown diagrammatically in Fig. 212. Two closely related mares, Pentoila's Favorite 164611 and Dope's Primrose 163421, born in the spring of 1920, were purchased from Ohio State University in 1923. The dam of the latter was the maternal granddam of the former, while the maternal great-grandsire of both was the same animal Diamant 30018, and both mares were sired by Libretto 121447. They therefore were 40 per cent related. Both mares were in foal to Colin 166024, a grandson

of Carnot 66666, when purchased and dropped filly foals, Lilly and Rose. These two mares (see Fig. 214) together with their filly foals appeared to be an excellent foundation for a band of Percherons together with a good homebred mare Daffodil's Belle.

However, the Dope's Primrose line quickly faded out. She was fifth Futurity filly at the International in 1921, fifth three-year-old mare at Ohio State in 1923, second aged mare at Eastern States Exposition in 1926. Besides her daughter Rose by Colin born in 1924, she left two

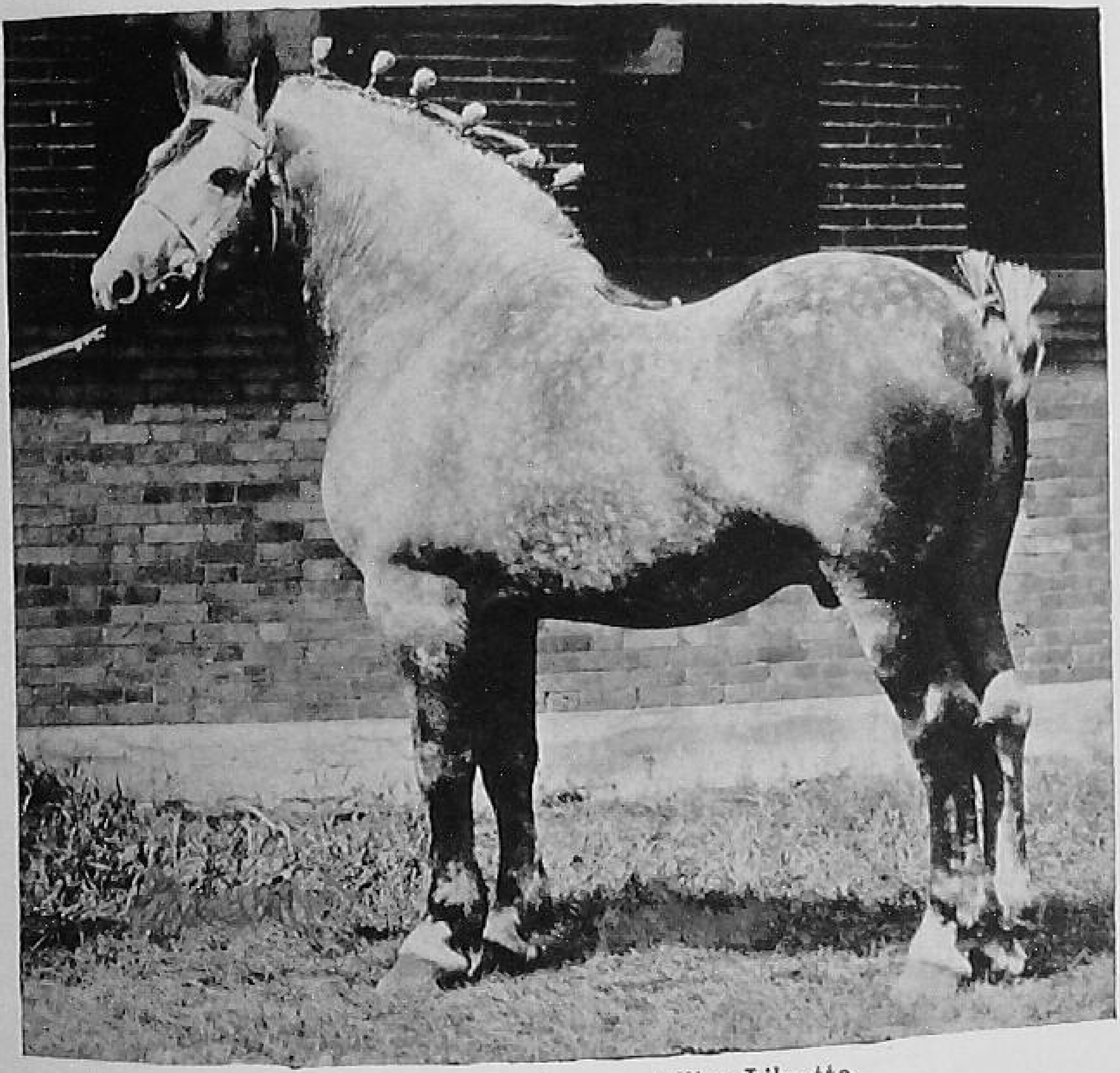

FIG. 213.—Percheron stallion Libretto.

colts by Revelation 181000, called Bay State Reliance 204527, which was first as a colt in 1930 and as a two-year-old stallion in 1932 at Eastern States and sold as a stallion, and Jerry, a male born in 1927 and used on the farm as a gelding. She did not conceive to breedings in 1924, 1925, 1928, and 1930 and bore a dead male foal in 1928. Her daughter Bay State Rose 186214 bore a male colt in 1928 that was altered. She failed to breed in 1928 and thereafter was used as a work horse until 1938 when she was sold. Dope's Primrose was sold in 1932. This mare, although a good individual and purchased as a foundation mare, made no contribution to the herd, and her line has entirely disappeared.

The other mare, Pentoila's Favorite, has been a fairly successful brood mare through having left one really good daughter Bay State Lilly 186213 by Colin in 1924. Pentoila's Favorite left 2 other daughters, Favorell and Novelle, by outside studs, which were not kept because of deficiencies in type, as well as 2 by Revelation 181000, *viz.*, Rosalind in 1928 and Rosabelle in 1929. Rosabelle dropped 1 filly foal that was sold, and she herself was sold in 1934. Rosalind dropped 3 dead foals, also 2 that went bad behind and 1 filly that was sold. In addition to

FIG. 214.—Foundation mares, Dope's Primrose and Pentoila's Favorite.

these 5 females, Pentiola's Favorite also dropped 5 stud foals, 1 of which died as a foal, 1 was altered, and 3 were sold as stallions. Pentoila's Favorite was first-prize filly foal at the Ohio and Indiana State Fairs in 1920, third filly at the Percheron International Futurity in 1921, junior and reserve champion at Indiana in 1921, first-prize aged mare at Eastern States in 1924.

Bay State Lilly 186213, a daughter of Pentoila's Favorite born in 1924, has been one of the most outstanding brood mares at the University of Massachusetts. She was first-prize mare in 1931 at Eastern States, first and grand champion in 1932, second-prize mare in 1933 and 1934, and first-prize mare and foal from 1928 to 1933, inclusive. Four of her sons have been sold as stallions (Review, Renown, Leander, and B. S. Laletto); 2 were working geldings on the farm (Rob Roy and Let's Go).

One daughter, Lillian, which had been first as a filly and yearling at Eastern States and second as a two-year-old, was sold.

Two other daughters of Lilly, Laura and Lady, by Revelation 181000 have been used as brood mares at the University of Massachusetts. Laura was third-prize filly foal at Eastern States Exposition in 1931, first-prize yearling in 1932, and stood second in 1933, first in 1934, second in 1935, fourth in 1936, second in 1937, and first mare and foal

Fig. 215.—Percheron mare Bay State Lilly.

in 1940. One son, Leader, by Lafayette 204281 and one daughter, Lala, by Laletto 208524 have been sold as breeding animals, and one daughter, Laurel, by Dragon Jr. 113939 and 2 by Laletto 2085424, Leta and Laurette, were brood mares on the farm. Their type through their rear quarter and the set of their hind legs, however, resulted in the discard of this entire line.

The other retained daughter of Lilly was called Lady. She was first filly foal and junior champion at Eastern States Exposition in 1932, first in her class in 1933, second in 1934 and 1935. Her first colt in 1935 by Dragon Jr. was altered, her second and third colts by Laletto in 1936 and 1937, Lena and Lady Lou, are brood mares on the farm, the latter having been first-prize two-year-old mare and junior champion at

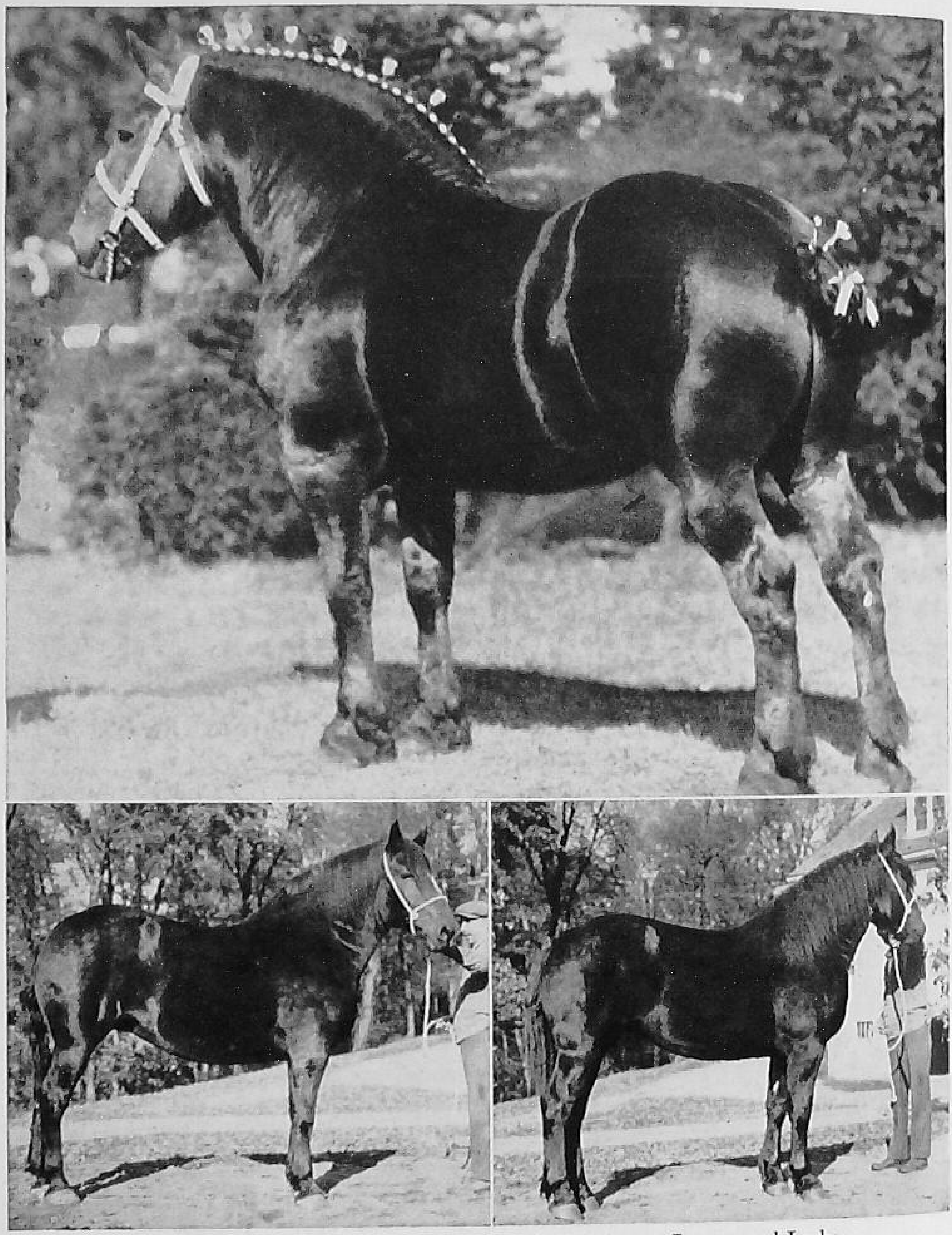

Fig. 216.—Revelation and his two best daughters, Laura and Lady.

Eastern States Exposition in 1940. Lady was sold in 1938 because of a bad front foot.

Lena and Lady Lou (full sisters and daughters of Lady) are still on the farm, and at present all our horses trace to them with the exception of two.

Lena had KonLena and KonLeader in successive years, both sired by

Konchapet and also had Konilla by the same stallion. When mated to Konhysop, she had Lensop, a young mare still on the farm; and when mated to Koncarno, she had another filly, Carno Carrie, that we had to destroy after she broke her leg. For the last two years Lena has had filly foals by Konhopecar II. The first one, Lorna, was Junior Champion mare at Eastern States Exposition in 1949 and won her class of eight yearling fillies. The second filly, Lucille, shows a great deal of promise, and we expect much from this pair of full sisters in our breeding program. In this same family line, Konilla has had a stallion foal that was sold as a gelding and has had a filly, Hopeful, by Konhopecar that has been discarded; she was one of the poorest in size and type of five good fillies by Konhopecar II. Lensop had one filly by Konhopecar II that we call Hylea. We, therefore, have Lorna, Lucille, and Hylea as potential female breeding replacements that trace to Lena.

Lady Lou had KonLouis, a gelding, that we disposed of and KonLady, both sired by Konchapet. KonLady is a brood mare on the farm and foaled with twins prematurely in 1948. Lady Lou had two fillies by Konhysop that are both brood mares on the farm; Lousop and Konhysop's Lady. Lady Lou had a stud foal by KonCarno that we altered, and now she has a promising yearling filly named Louise, sired by Konhopecar II. Lousop had a stud foal by Konhopecar II that was sold as a breeder, and Konhysop's Lady has a filly foal, Kathleen, sired by the same stallion, that probably will be retained as a brood mare.

The third foundation mare, the homebred Daffodil's Belle, has been an average good brood mare. Her daughter Betsey by Revelation 181000 was second-prize foal at Eastern States in 1931, but she and all her offspring have been sold. The other daughter, Belle, also by Revelation 181000, was not shown. Belle had a daughter, LaBelle, by Laletto and four other foals. LaBelle is the only one present as a brood mare on the farm. LaBelle, when bred to Konhopecar II, had a filly, Lana, that in 1949, as a yearling, was second in a class of eight fillies at Eastern States Exposition.

So, after a start with the foundation mares in 1923, and using nine different stallions, we now have two good full sisters—Lena and Lady Lou—as brood mares on the farm. Both are good-type mares and have transmitted satisfactorily; so satisfactorily that at present all of our Percherons, except LaBelle and Lana, trace to Lena and Lady Lou. LaBelle is a rather plain-bodied mare but has high-quality underpinning. When she was mated to Konhopecar II, she had Lana, and we are much pleased with her individuality.

Our younger mares, Konilla, KonLady, Lensop, Lousop, and Kon-

hysop's Lady are all relatively untried as breeders, and we have much to learn about their transmitting ability.

We have bred and raised a lot of horses since 1923. Most of these animals have been used on the farm and have done their work in an acceptable manner. The stallions have been carefully selected in regard to their individual type and have cost from $1,000 to $1,500. Revelation 181000 was used for 7 years (1925 to 1932) and sired two very good offspring, Laura and Lady, a lot of good ones, and some poor ones. He was an imported horse that stood second to Hesitation, the grand cham-

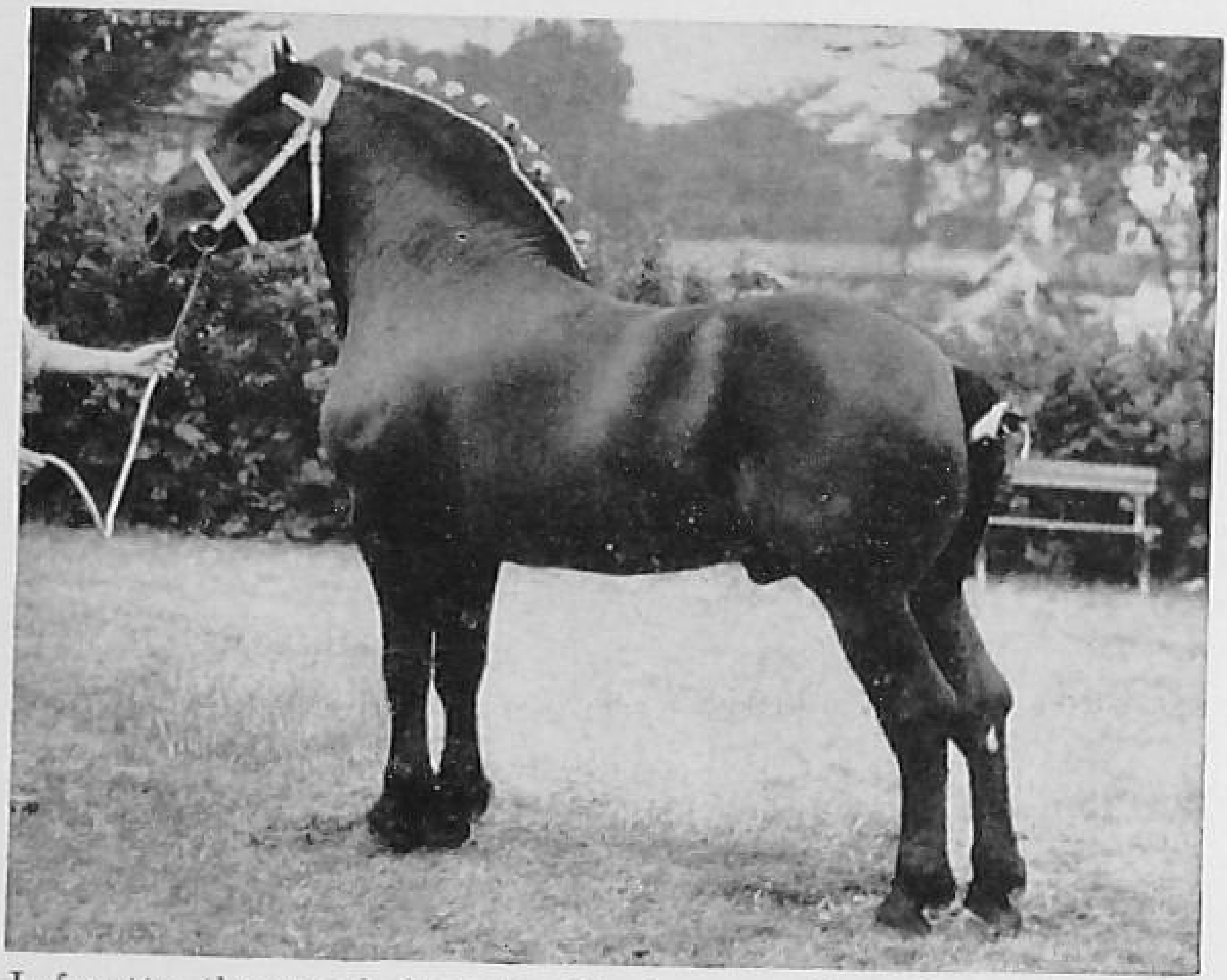

FIG. 217.—Lafayette, the grand champion Percheron stallion, Eastern States Exposition, 1933. Owned by Massachusetts State College.

pion at the International in 1923. He was grand champion at the Eastern States Exposition in 1925, 1926, 1927, and 1930.

Lafayette 204281, a son of Sir William 168112, he by Laet, was used from 1932 until his death from coronary thrombosis in 1935. He was grand champion at the Eastern States Exposition in 1933 and 1934. He was an excellent individual but left no impression in our herd, leaving only one daughter which was culled.

Laletto 298524 was purchased in 1935 and used until the purchase in 1945 of Konhopecar II. Like Lafayette 204281, Laletto is a grandson of Laet 133886, and his dam is by Libretto, the sire of the two originally purchased mares. There is, therefore, just a slight trace of line breeding to Libretto 121447 in the pedigrees of the daughters of Laletto at present in the herd. Laletto was third-prize aged stallion at Eastern States in 1936 and 1937 and senior champion in 1941.

Konchapet, Konhysop, and Koncarno, all sons of Koncarcalyps, bred by Madrey Farms, were used successively in our herd. We purchased Konhopecar II (by Koncarcalyps and out of Carnona IV's Hope) in 1945 as a yearling. He is a full brother to the Lynnwood Farm's horse, Koncarhope, that was grand champion at the National Percheron Show in 1947. We showed Konhopecar II to the grand championship in 1949 at Eastern States Exposition, where he defeated another good son of Koncarcalyps, Koncarno, and also a good son of Topper, owned by

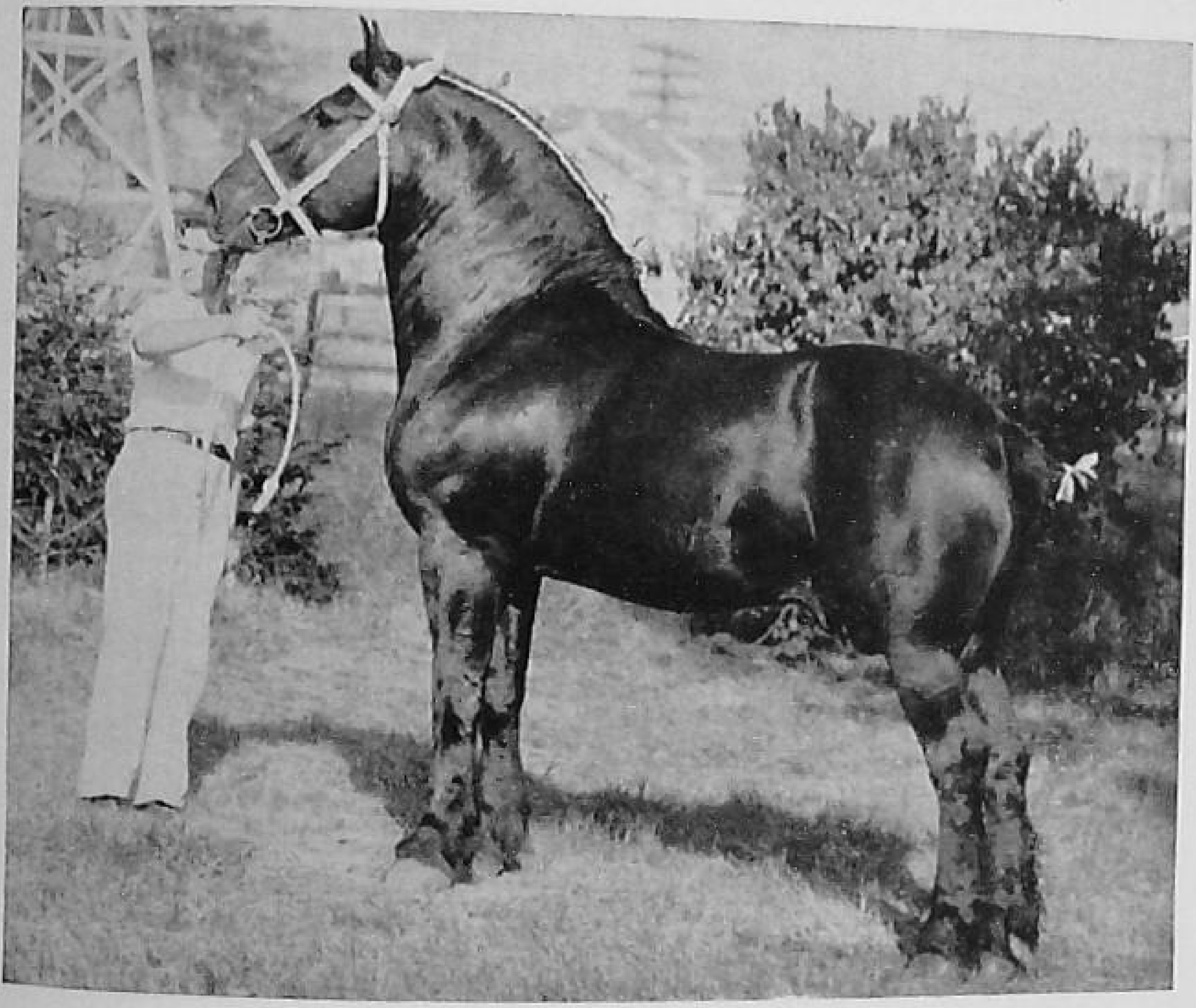

FIG. 218.—Percheron stallion Laletto.

Floyd Hill of North Woodstock, N.Y. We are expecting a great deal from the get of Konhopecar II. His yearlings and foals at present show every indication of general improvement over our brood mares.

As is indicated in the above discussion, some of the female lines are better than others. A glance at Fig. 212 shows that practically all the animals represented trace to old Pentoila's Favorite. The job of breeding and improving horses is not an easy one. The story has been told here for the purpose of illustrating the fact that rapid progress in the breeding of a species of animals that reproduce at such a slow rate as does the horse is hardly to be expected.

Selecting the Fillies to Save.—Only after a breeder has made a close study of the mares in his own band with suitable records and tabulations of their strong and weak points is he in a position to start on his search

for a stallion to mate with them. It is obvious, of course, that the male should be selected both on the basis of holding the desirable qualities which the breeder already has and also, and more especially, of bolstering the weak points shown by the mares. The mares at the University of Massachusetts have from the beginning been a little too light in bone and a little too shallow to suit us. In addition there is a tendency for the hind legs to be a little close together and not to set under the horse as much as they should. In our search for our next stallion, these points will receive major attention.

In selecting mares or fillies either from outside or in one's own herd, acceptable type for the class of horse concerned should, of course, be the first criterion regardless of the fact that mares do not always breed exactly as they look. In other words, one has a greater expectancy of getting drafty offspring from draft mares than from Thoroughbreds, and vice versa.

In addition to acceptable type, one should try to select from good female lines in which as many as possible of the animals have been of the desired type. An obvious weak point in the University of Massachusetts horses, as discussed above, is the fact that Pentoila's Favorite had 4 mediocre daughters and 1 good one, Lilly. Lilly in turn had 2 mediocre daughters and 2 good ones, Laura and Lady, and the latter, a somewhat poorer individual, is evidently transmitting in a more acceptable fashion than her somewhat superior typed sister, Laura. In this whole female line, there are evidently both good and bad genes, the former not being so numerous as one might wish. It is very important, therefore, that both the direct ancestors (those occurring in the pedigree) and the collateral relatives (half brothers and sisters, cousins, aunts, uncles, etc.) receive some consideration. Because, generally, only the most acceptable animals are saved and used for breeding purposes, the pedigree of the direct ancestors of an animal is bound to look pretty good and will tell us, in general, the best that we can expect. The collateral relatives, on the other hand, which do not generally appear in the pedigree or, if included, contain only the desirable references, will tell us some of the bad things we may expect by selecting their family. The pedigree of the University of Massachusetts filly Leta can be made to look very good, as is shown in Fig. 219.

The pedigree (Fig. 219), with some of the better show winnings listed, looks very good. How about some of the collateral relatives? Pentoila's Favorite had 1 good daughter Lilly and 4 not very good ones; 1 good son, 2 or 3 average ones, and 1 poor one. Lilly had 2 good daughters and 2 mediocre ones, 6 sons ranging from good to poor. Revelation had quite a range of offspring, making his total breeding value about average.

Laura's offspring on the whole (4 daughters and 1 son) have not been nearly so good as their dam in draft quality. Laletto has sired a range of offspring from very good to very poor. Leta, the filly pedigreed in Fig. 219, is a fairly good individual, but she is not so good as Fig. 219 makes her appear, and, although she has some good genes, it would seem from a study of her collateral relatives that she probably also has a lot of poor ones and would probably not be a particularly successful breeding

- **Leta** 1st prize foal 1937
  - **Laletto** 2d prize Ohio, Indiana 1935, 3d prize Eastern States Exposition 1936, 1937
  - **Laura** 1st Eastern States 1932; 2d Eastern States 1933; 1st Eastern States 1934; 1st Eastern States 1940
    - **Revelation** 2d International 1932; Grand champion Eastern States Exposition 1925, 1926, 1927, 1930
    - **Lilly** 1st prize Eastern States 1931; 1st and grand champion Eastern States 1932; 1st mare and foal 1928–1933, inclusive
      - **Colin**
      - **Pentoila's Favorite** 1st filly Ohio and Indiana 1920; Junior and reserve champion Indiana 1921; 1st mare. Eastern States Exposition 1924

Fig. 219.—Good-looking pedigree of Leta.

or transmitting mare. Complete pedigrees in terms of record of performance of both direct and collateral relatives can be an important aid to selection based first of all on individuality.

The real test of a breeding animal is, of course, its ability to transmit its own desirable qualities. This is the progeny test, which should be utilized wherever possible to do so. If we can find good individuals, whose complete pedigrees will bear the light of careful scrutiny and who have demonstrated their ability to transmit their own good qualities, we are on perfectly sound ground in making our selections, although we have yet to learn how this triply desirable animal will "nick" with one of our own. Obviously, it is not always possible to get all this information,

in which case a breeder should get all the information available and then "cross his fingers" until he sees how things turn out.

In the selection of brood mares, it is essential that attention be given to their probable and actual ability to bear young over a long period of years. Their probable ability in this regard can best be judged from their complete pedigrees (both direct and collateral relatives). In other words, in the selection of mares one should select only in families that have a high natural rate of fertility. Like all other attributes having a genetic basis, this varies among different families in all the classes of livestock. Demonstrated abilities by the direct and collateral relatives is the best guarantee that a breeder can get for any new animal going into his band of females.

Actual ability to reproduce can be ascertained from the performance of older mares as well as from current examinations of their genital tracts by competent veterinarians, and the latter type of examination can and should be used on young mares.

Finally, in the selection of mares or fillies that hard-to-describe quality of femininity should receive considerable emphasis. The general term for it is probably *quality*, as evidenced in fine texture of bone (different, of course, with different types of horses) and fineness of hide and hair, together with indications of alertness and intelligence and a certain nobility of carriage and demeanor. The mare should be well balanced throughout, with a roomy middle and ample width through the hips and croup, and must have a sound, well-developed udder.

Selecting the Stallion.—The safest plan in securing a stallion is obviously that of getting one that has already demonstrated his ability as a sire in the type and performance of his get, in other words, a proved sire. Unfortunately not many good, proved stallions are available at any price. Most breeders, therefore, will have to select and use young, unproved studs.

These should be healthy, of the desired type and disposition from a naturally fertile strain. Preferably they should be by a proved stallion, the majority of whose offspring were desirable and out of a daughter of a good proved stallion, said daughter having preferably demonstrated her ability to transmit desirable qualities to her offspring. Admittedly, such animals are scarce, complete records of ancestors not generally available, etc. Nevertheless we must make a start sometime in getting such information, and it is unlikely to become available until prospective buyers start asking for it.

Just as indications of femininity are desired in the female, so do we desire indications of masculinity in the stallion. Here we expect a little more compactness and scale, a little heavier bone, a well-developed

forequarter and chest. We want spirit and masculinity in our stallions but of a sort that proper training has rendered obedient.

Sire Indexes in Horses.—As yet few objective measurements of performance that might serve as a basis for an index have been developed for the horse. H. H. Laughlin has evolved a mathematical yardstick for measuring racing capacity in the Thoroughbred through a study of the breeding and racing records of some 10,000 of these animals. He has measured quality of performance for a single race on a definite mathematical scale by developing correction factors for sex, age, weight carried, distance run, and speed, on the basis of actual performance of this breed under varying conditions and yielding standards that are the "smoothed best" which the breed has accomplished up to the present time. By means of such standards the true racing capacity of any horse can be measured, and, if he runs a sufficient number of races under standard conditions, the one figure for racing capacity (derived from the several "quality-of-performance" figures for separate races) can be compared with a similar figure for any other horse, and the question as to which was the better racing horse can be definitely answered, although the two horses may have never raced against each other.

When the racing capacities of a male and female together with their close, direct, and collateral relatives can be ascertained, then it is possible to formulate a futurity index or hereditary-promise level for their offspring. Because racing capacity involves the whole organism, it is reasoned that multiple genes are concerned, and therefore equal weight is given to both the sire and dam in arriving at the futurity index of their offspring. In this system the breeding factor of the sire is obtained by taking one-third of the average racing-capacity figure of his sire and dam plus one-third of the racing capacity of the sire himself plus one-third of the average racing capacity of the foals that he has already sired. The breeding factor of the dam is arrived at by a similar procedure, and the average of the sire's and the dam's figures is called the futurity index of their potential or actual offspring. This "prediction-index, when it contains only a few ancestors, each doubtfully stressed, gives a low prediction-value; but when it comprises a highly representative group of close antecedent blood-kin, each properly stressed, then the prediction-value of the specific formula is high."[1]

It would, of course, be possible to work out similar prediction values for any type of racing horse, where the one criterion for selection is that of speed, or for show horses, where the criteria are type, action, and

[1] Laughlin, H. H., Racing Capacity in the Thoroughbred Horse, *Sci. Monthly*, **28**:210, 310, 1934.

manners, provided accurate and complete records of performance are available.

Phillips, Brier, and Lambert have made some preliminary studies of tests designed to measure the speed and efficiency of light horses. The tests were designed to measure speed, both at the walk and trot in carriage and at the trot under saddle, length of stride, and respiration and heart rate before and after exercise.[1]

From the results it is evident that tests designed to measure speed, length of stride, and respiration and heart rate are subject to rather wide variations when applied to the same horse at different times. It is apparent, therefore, that, if such tests are used for the purpose of detecting differences between horses, the tests must be repeated several times under carefully controlled conditions. However, the degree of accuracy required will depend upon the magnitude of the differences that it is desired to detect. In most of the analyses presented here, the variability of the material used (i.e., of the 14 horses) relative to the various sources of error was high enough that the observed differences between horses were significant. In a more uniform group of horses it would probably be necessary to improve the accuracy of the test in order to differentiate with any degree of certainty between animals with respect to any given character.

It should be emphasized that the results presented in this bulletin deal only with the degree to which results of each of the tests agree when obtained on the same horses at different times. Before these tests, or any other tests of performance, should be applied generally, careful studies are needed to determine the relationship of the tests to actual performance under practical working conditions.

Although the machine has replaced the horse as a source of draft power to a very considerable extent, there is unmistakable evidence that interest in light horses for pleasure and sport is on the increase. No better safety valve for the effects of our high-speed, machine civilization can be imagined. It is to be hoped that much of the former breeding of draft horses in our farms can be gradually replaced with the breeding of light horses. This is a new field which has opened up in the past few years and one that seems to hold much in the way of possibility, especially for farmers located near the large centers of population.

In the draft horse, we also need objective tests for measuring working abilities. These animals exist for the one purpose of doing useful work. As stated by Phillips, Krantz, and Lambert,[2]

[1] Phillips, R. W., Brier, G. W., and Lambert, W. V., A Study of Some Problems Involved in Measuring Performance in the Horse, *U.S. Dept. Agr. Bur. Anim. Ind.* Mimeographed Rpt.

[2] Phillips, R. W., Krantz, E. B., and Lambert, W. V., The Accuracy of Measurements and Scores of Draft Horses, *Amer. Soc. of Anim. Prod. Proc.*, 1938, p. 82.

Objective measures of the characteristics which contribute to maximum ability to do work are badly needed. Such measures might include maximum pulling ability for a short period of time, staying power with a heavy load over long periods, walking speed with a standard load over a given distance, and ability to maintain weight doing a given amount of work with a given allotment of feed, along with careful records of the occurrence of soreness and unsoundnesses. When such methods are developed and a sufficient number of records is obtained under standard, experimentally controlled conditions of training and testing, and the animals used have been scored and measured at comparable ages, it will be possible to arrive at some estimate of the value of any given measure or score.

The dynamometer is available and has been used for many years to get the maximum pulling ability of horses for a short period. Records of these contests together with measurements of the animals competing have shown definite correlations between height and weight and ability to pull, but no other measurements have shown definite positive correlations. "Staying power with heavy loads over long periods" and "walking speed with a standard load over a given distance" might also be secured by means of the dynamometer.

So far as the writer knows, the dynamometer has not as yet been used in any constructive manner as an aid in the selective breeding of draft horses. The dynamometer contests[1] are a very interesting sporting event and generally draw a much larger crowd than does the orthodox judging of horses on the basis of type. In fact, it has happened more than once that the type judging has had to be temporarily suspended until the breeders and showmen of the purebreds have returned from watching the pulling contest. In other words people in general are more interested in seeing what a horse can do than they are in admiring him for what he may look like.

Type in Horses.—Horses have been selected on the basis of the type best suited to perform given tasks for hundreds of years. This has led gradually to the creation of distinct and separate types for racing, riding, driving, and pulling. Selecting the speediest horses gradually produced the racehorse type, selection for power gradually produced the draft-horse type. The speed and saddle types are now definitely established, and there seems to be little prospect that they will be changed in any fundamental way. The task of the future in these types, then, is further refinement to add slightly to their speed, symmetry, balance, action, and behavior; and by means of keener selective tools based on records of performance, measurements, and progeny tests to render them more homozygous for the respective qualities desired.

[1] See Phillips, R. W., Madsen, M. A., and Smith, H. H., Dynamometer Tests of Draft Horses, *Utah Agr. Expt. Sta. Cir.* 114, 1940.

The draft horse was created by selection for the particular purpose of moving heavy loads at a fair speed. For this task the criterion was the greatest weight possible in the smallest compass. The heavy draft horse was a remarkably efficient animal for the job he was supposed to do. The railroads, trucks, and tractors have made their appearance during the past 100 years, however, to challenge the horse in this field, and largely because of their greater speed they have supplanted him so that the market for the ton-upward horse has shrunk almost to the vanishing point. Draft-horse type, in other words, is changing to a somewhat smaller, more active model, with greater quality. In particulars, the type will remain what it always has been, a short, compact, well-set-up, and straight-moving type, but, in place of weighing from a ton upward, he will weigh from a ton downward. He will be a medium-sized draft horse, since the city market for the heavy sort has disappeared, the farmer never did like the extremely big ones, and in so many instances now power machinery has to do the very heavy work. The new type will stand 15:3 to 16:2 hands, the stallion weighing 1,900 to 2,100 lb., the mares 1,700 to 1,900 lb. in good condition.

There are two ways of creating such a horse, one by mating large stallions to small mares (or small stallions to large mares) and the other by mating medium-sized stallions to medium-sized mares. If the former method is used, and we put in the two extremes, we will generally get the mean in the immediate offspring, but the mixed inheritance of these animals can be expected to come out in all sorts of combinations in their offspring. In other words, we can expect to have to do a lot of weeding out if such a plan for creating the medium-type horse is used. Because the average run of farm mares tends to be on the small side, there would still seem to be a place for the good-sized stallion of good quality.

The other plan of mating medium size to medium size should give less extreme variations and lead more quickly toward the desired goal.

With the system either of mating unlikes to produce a medium or of mating intermediates in types, it goes without saying that selection must be practiced and the offtype animals discarded. Less of this will be necessary with the matings of animals that resemble each other closely in general type. One should not deceive himself, however, by thinking that two animals which are similar in appearance are also similar in their genetic make-up. Many different combinations of genes may give the same general phenotypic appearance. We must remember that, in dealing with commercially important characters of our animals, we are probably dealing with hundreds or thousands of genes. This is very different from crossing a rough, white guinea pig (*RR bb*) and a smooth, black one (*rr BB*) and getting rough, black offspring (*Rr Bb*). And even

in this simple case, dominance interferes with our progress, because we cannot distinguish offhand between the following rough, black guinea pigs (*RR BB*), (*RR Bb*), (*Rr Bb*), (*Rr BB*). We have no conception of the dominance, partial dominance, epistatic, and other probable interrelations involved in the thousands of genes in our larger animals. There are many combinations of coins that will make a dollar, *e.g.*, 10 pennies, 4 nickels, 2 dimes, and 2 quarters, or 5 pennies, 3 nickels, 3 dimes, and 1 half dollar, etc. Likewise many combinations of genes may give the same phenotype.

If animals are to breed true, they must be made homozygous in the bulk of their genes. Mating animals which are alike phenotypically will have little effect in making them homozygous in their genes, and likewise mating unlikes will have little effect in making them more heterozygous in their genes. In short, whatever system is adopted for attempting to create a true-breeding strain of intermediate-sized draft horse must involve both selection and some form of inbreeding in order to render the animals relatively homozygous or in the breeder's language to "fix the type."

This whole business of changing the type (weight) of our draft horses means many a headache for the judge in the show ring. It is going to take real courage to turn down a good big horse in favor of a good medium-sized one. The big one will excel in weight and draft power, the smaller one to offset this should be expected to excel in action and movability. Care must be exercised too that the desire for somewhat less weight than formerly does not express itself in either a chunk, easy keeping to be sure, but generally lacking in movability, or in an upstanding, light-boned, and light-middled animal which is apt to be a hard keeper, lacking in power and stamina, although probably excelling in freedom of action or movability. It is in just such situations as this one involving a change in type that the art of the breeder has its best opportunity of expression. If the art is backed up by or based upon a sound knowledge of the genetic principles involved, it will eventually evidence its inherent soundness. Art alone, however, is not enough (or it works too slowly with too many mistakes); nor is a knowledge of principles in itself enough. For constructive breeding at a tempo to suit the modern age both art and science are essential.

Breeding Efficiency in Horses.—In order that the breeder may have a clear picture of the breeding efficiency of his stallions and band of mares, careful records should be kept of the occurrence of heat periods in the mares, number of services required to settle each mare, percentage of mares settled by each stallion, birth weight of foals, duration of gestation, etc.

A study[1] of the breeding performance of 43 mares at the United States Morgan Horse Farm, Middlebury, Vt., from 1928 to 1938 shows that

132 mares conceived, foaled, and raised their foals.
 10 mares conceived, foaled, but foals died before weaning.
  6 mares conceived but aborted.
 73 mares failed to conceive.
221 total mares bred.

Summarizing, we see that 221 breedings produced 132 foals which lived—a breeding efficiency on the part of these mares of 59.7 per cent in terms of livable foals.

Morgan Horse Breeding by the U.S. Department of Agriculture.—The United States Morgan Horse Farm was established at Middlebury, Vt., in 1907, as a result of a gift from Col. Joseph Battell. The farm at present is composed of approximately 1,000 acres. The primary object of the farm is to conduct research that will yield results of value to all horse breeders and users. Since Morgans were already on the farm, it was logical that the work be done with them. The use of Morgans is incidental to the main objective of conducting research that will yield information of value to horsemen. Pasture improvement, research, observations on reproduction, devices for training and testing are studied and data collected and analyzed.

Performance testing was initiated in 1940 with the horses in an attempt to learn more about the suitability of the individual, line, or sire group for pleasure purposes, riding, or driving. Objective measures—qualitative and quantitative—have been made and some little data collected as results of the tests. At Middlebury the horses are scored for conformation, general appearance, feet and legs, and action at one year, two years, and three years of age. All horses are measured for such things as height at the withers; depth of chest, heart girth; circumference of the fore cannon, rear cannon, etc. Weight records are maintained from birth up to three years of age on all horses.

The actual performance tests are designed to give a definite measure of speed for a mile at the normal walk and trot and the length of stride of these gaits, both under the saddle and in the harness. Each horse carries 20 per cent of its body weight under the saddle and pulls 60 per cent of its body weight in the harness. These tests are made on a ⅛-mi. track.

Endurance is measured under the saddle on a cross-country ride of about 11 mi. Approximately 50 per cent of this distance is covered

[1] LAMBERT, W. V., SPEELMAN, S. R., and PHILLIPS, R. W., The Reproductive History of the Stud at the United States Morgan Horse Farm from 1928–1938, *Amer. Soc. Anim. Prod. Proc.*, 1939, pp. 358–365.

at the trot, 10 per cent at the canter, and 40 per cent at the walk. In addition to the time record, each horse is scored for ease of handling, response to commands, degree of fatigue, and ease of gaits by the rider. Recuperative power is measured in harness by a test on the track at the trot for 5 mi. This is done by studying data on respiration and heart rates as well as time elapsed in completing the distance.

Results to date on the above types of performance studies are an approach to the many problems involved. It is obvious that there is variation from year to year and variation due to riders and trainers. Every attempt is being made to standardize these environmental influences as much as possible. Temperament or the "desire to go" undoubtedly has considerable effect on the performance of the individual horses. It has been found that temperature and humidity also affect results greatly, particularly the endurance tests. Very many conclusions cannot be made until some of these variable factors are controlled even more than at present.

These performance tests and correlative studies involving them and other measurements are a complex problem. The results over the next few years should be of value to all breeders of horses for saddle purposes.

Summary.—We have seen in this chapter that in spite of drastic reductions in the numbers of horses in the United States during the past 30 years, due to the inroads of various forms of mechanized power, the horse is still very much with us as a source of power on the farm and is filling an ever larger place in pleasure and sport. In the past, selection of horses has been based almost wholly on individuality. Because inheritance in horses follows the one basic pattern found in all animate forms of life, we have now come to realize that sound selection must consider records of performance of direct and collateral relatives and of the animal itself in addition to the consideration of individuality. We are badly in need of practicable measures of performance in the horse. Only when these have been devised and put to work in the securing of essential records, and the records used intelligently, together with continued full considerations of individuality, will our selection in this class of livestock be on a sound footing. When the above methods have revealed the inherently better strains of horses, we will face the further task of intelligent line- and closebreeding, so that we may create fairly true-breeding strains.

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CHAPTER XXIV

RETROSPECT AND PROSPECT

We have now completed our discussion of the principles underlying the creation of better livestock. We tried to start at the beginning, to get some idea of the probable origin of life on the planet Earth something over 1 billion years ago. We concluded that something comparable to the gene must have appeared fairly early in this process. These entities, capable of certain reactions among themselves and with their immediate environment, the cytoplasm of the cells, and endowed with the power of exactly reproducing themselves, seem to have been proved without reasonable doubt to be the mechanism of inheritance in all living forms today.

From the point of view of logic, it seems probable that the genes have always performed this function. In the earliest stages, there perhaps was formed wave after wave of the simplest sort of living material that flourished for a short time and then quickly faded out of existence as living things without leaving offspring. At some stage, however, we must suppose that bits of this living material in some way became endowed with the property of reproducing themselves, so that as the old died, the new was born. Once started and with the occasional production of something a little different from the parent form we have the basis for an evolutionary process. At present, so far as we know, a new and somewhat different living thing can arise only from other living things by means of the genes. They are today the fundamental mechanism of life, as evidenced through reproduction. It seems likely that they have always fulfilled this role.

We hurriedly traced the process of evolution until it finally gave rise to the larger farm animals and to man himself. We sketched the story of man's progenitors until modern man, *Homo sapiens*, appeared on the scene some 25,000 to 50,000 years ago. Then we saw man take one of his greatest forward strides some 8,000 to 12,000 years ago when he began to domesticate plants and animals, which better ensured his food supply.

We then sketched the progress that man has made through historic time in breeding, selecting, and perfecting his animals for specific purposes, and finally we find ourselves in the twentieth century with well-nigh perfect individual animals in all the classes of livestock, but with

the average type and performance of our livestock well below an efficient and profitable level.

Our next task was that of learning some of the details of the workings of the intricate process of reproduction. In the lower forms of life, this process is relatively simple consisting merely of fission or division of the parent into two offspring. Next came budding, one or a few unspecialized cells having the power of creating a new individual. In time, specialized cells were developed for the reproductive function. Eventually, they came to be specialized in different ways, the union of two differentially specialized cells being necessary for the creation of a new life. Originally, these different cells were produced by the same organism, but they finally came to be produced by different members of the species, which gave rise to the sexes. At first, these male and female sex cells were passed to the exterior, where fertilization and growth took place. As organisms grew in complexity, so did the generative apparatus, so that in the higher forms of life we have, besides the glands producing the sex cells, a complicated mechanism of accessory glands and organs under the control of distantly located endocrine glands, with fertilization and embryonic development taking place internally, the latter proceeding for many months and resulting eventually in the birth of a completely organized, though somewhat helpless and dependent, individual.

The researches during the past half century, and particularly during the last decade, have done much to explain the reproductive processes and the factors which limit maximum reproduction.

One of the most amazing technological advances in animal production has been the development of techniques for, and the rapid acceptance by livestock producers of artificial insemination. The use of this method on a few thousand dairy cattle in the United States in 1938 had been extended to nearly 3 million in 1949, and it appears that, in some intensive dairy areas, artificial insemination may soon be the predominant method of breeding.

During the 10-year interval that the artificial insemination program has been developing in the United States, the methods of processing and utilizing semen have been greatly improved. Earlier estimates that the semen of one bull could be used to service 1,000 cows annually have been revised upward to 10,000 cows. Semen was at first diluted 1:4 and transported within a radius of 20 to 30 mi. The regular dilution rate is now 1:100, and experimental work indicates that it may be extended to 1:400 or even higher. Semen is now being transported between states by bus, rail, and air on a regularly scheduled basis.

Much progress has been made in storing sperm, but the maintenance of maximum fertility in stored semen leaves much to be desired. As

yet few samples of bull semen give satisfactory fertility when stored for more than 3 or 4 days and other farm animals even less. The fact that sperm *motility*, but not *fertility*, can be maintained for many months in quick-frozen semen; that sperm retain their fertilizing capacity for up to 5 months in the female reproductive tract of the bat; and that

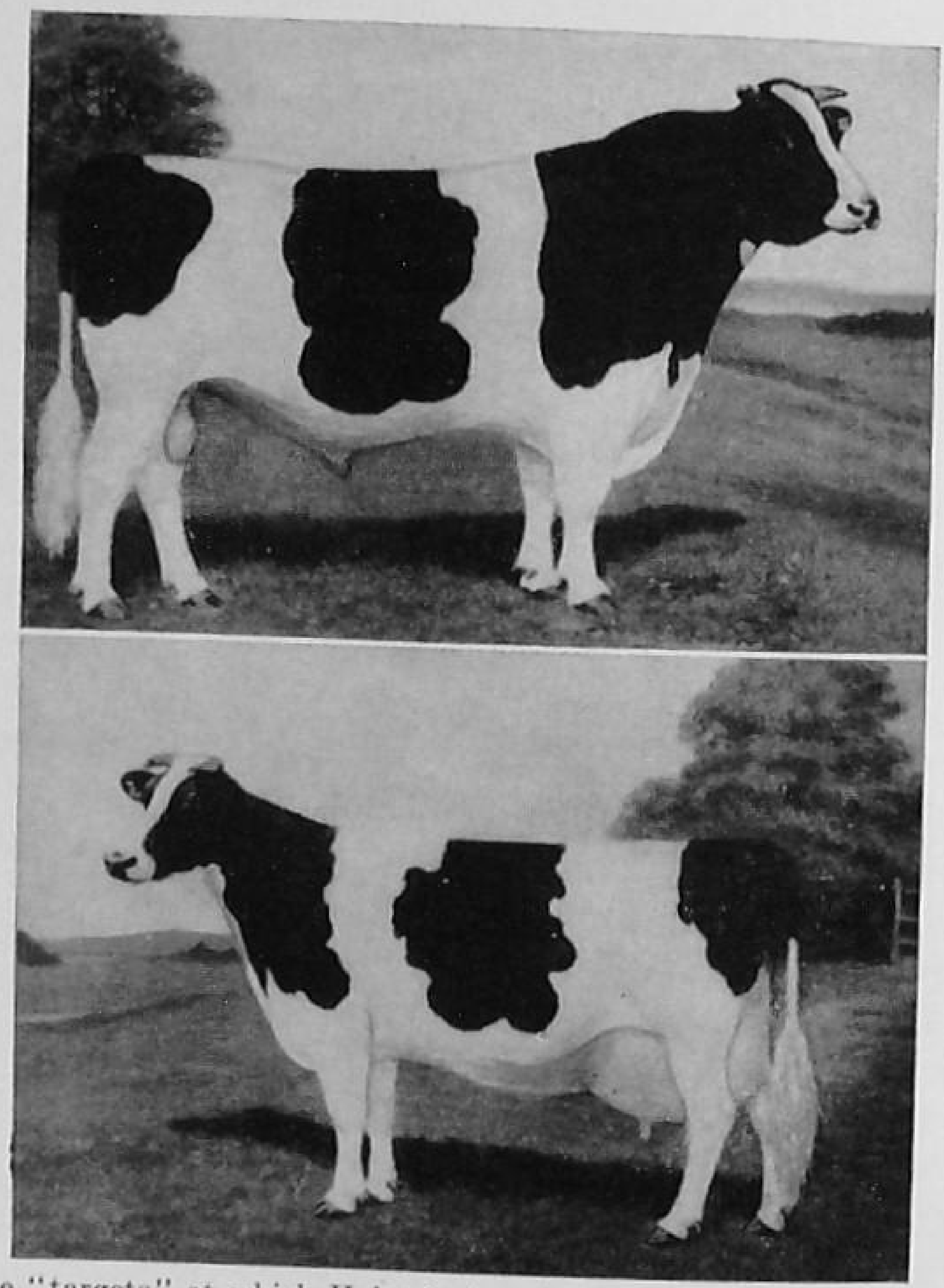

FIG. 220.—The "targets" at which Holstein breeders are shooting. Such models should prove invaluable in fixing type.

the queen bee can produce fertile eggs for 3 to 4 or even up to 7 years, indicates to the physiologist that there are broad horizons ahead.

The endocrine regulation of the testis is fairly well understood, but it is as yet impossible to completely regulate fertility in the male by artificial means. Too many sires are deficient in reproductive capacity. Whether their limitations are genetic, physiological, pathological or environmental remains to be learned. One of the important questions before attempting to restore fertility in males is whether or not the

cause is heritable. We cannot stress too much that breeding animals must first of all be of high fertility.

In the female the widespread use of the principles of breeding management now at hand would increase the breeding efficiency of most herds and flocks. Unfortunately, 100 per cent efficiency is seldom achieved at present. One of the most puzzling problems is the failure of "apparently normal" animals to conceive.

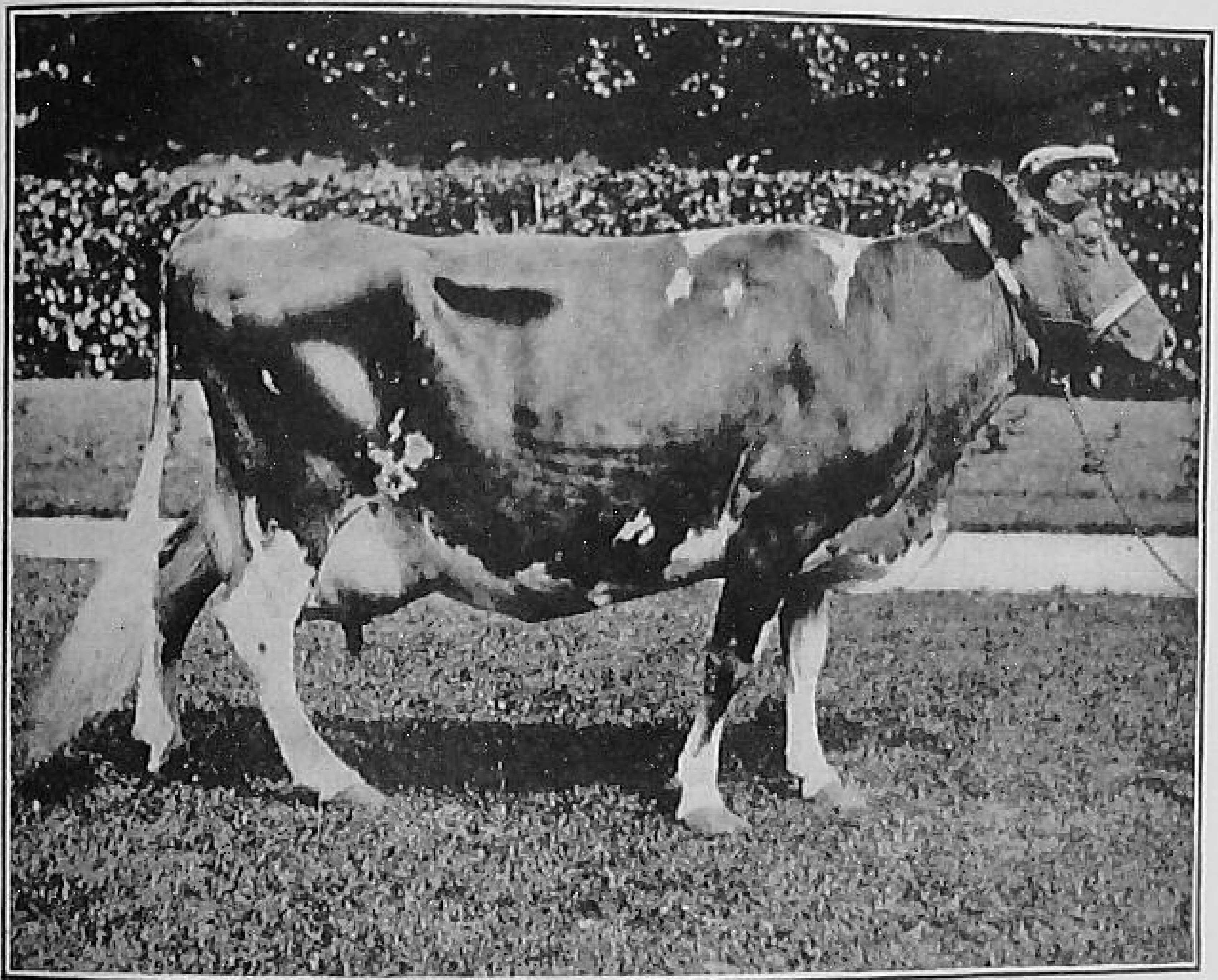

FIG. 221.—May Rose II, foundress of the May Rose family of Guernseys, noted for type as well as production. (*Courtesy of American Guernsey Cattle Club.*)

As new information and techniques become available, the diagnosis of reproductive disturbances becomes more exact. Difficulties which were previously unrecognizable are now becoming known, and it is hoped that methods of correction will follow.

The recovery and transfer of fertilized ova from one rabbit to another has been repeatedly accomplished for nearly three-quarters of a century. Much interest in the possibilities of utilizing this technique in cattle is being shown. It is well known that the ovaries of cattle, sheep, and other species can be caused to produce ova in greatly increased numbers. It is likewise known that many of these ova do not develop normally.

As described in previous chapters great numbers of fertilized ova may be produced by appropriate endocrine treatment, and in a few instances fertilized eggs have been successfully transferred from one sheep to

another. These techniques are far from the practical stage in 1949, but much optimism, especially in the popular press, is being shown.

Artificial parthenogenesis has already been achieved in one mammal, the rabbit. Whether or not a scientific procedure for accomplishing this in the larger animals will ever be achieved remains to be seen. What a boon it would be, for instance, in cattle if a particularly good cow could be made to reproduce parthenogenetically, provided, of course, that she herself was relatively homozygous for the desirable genes, because we

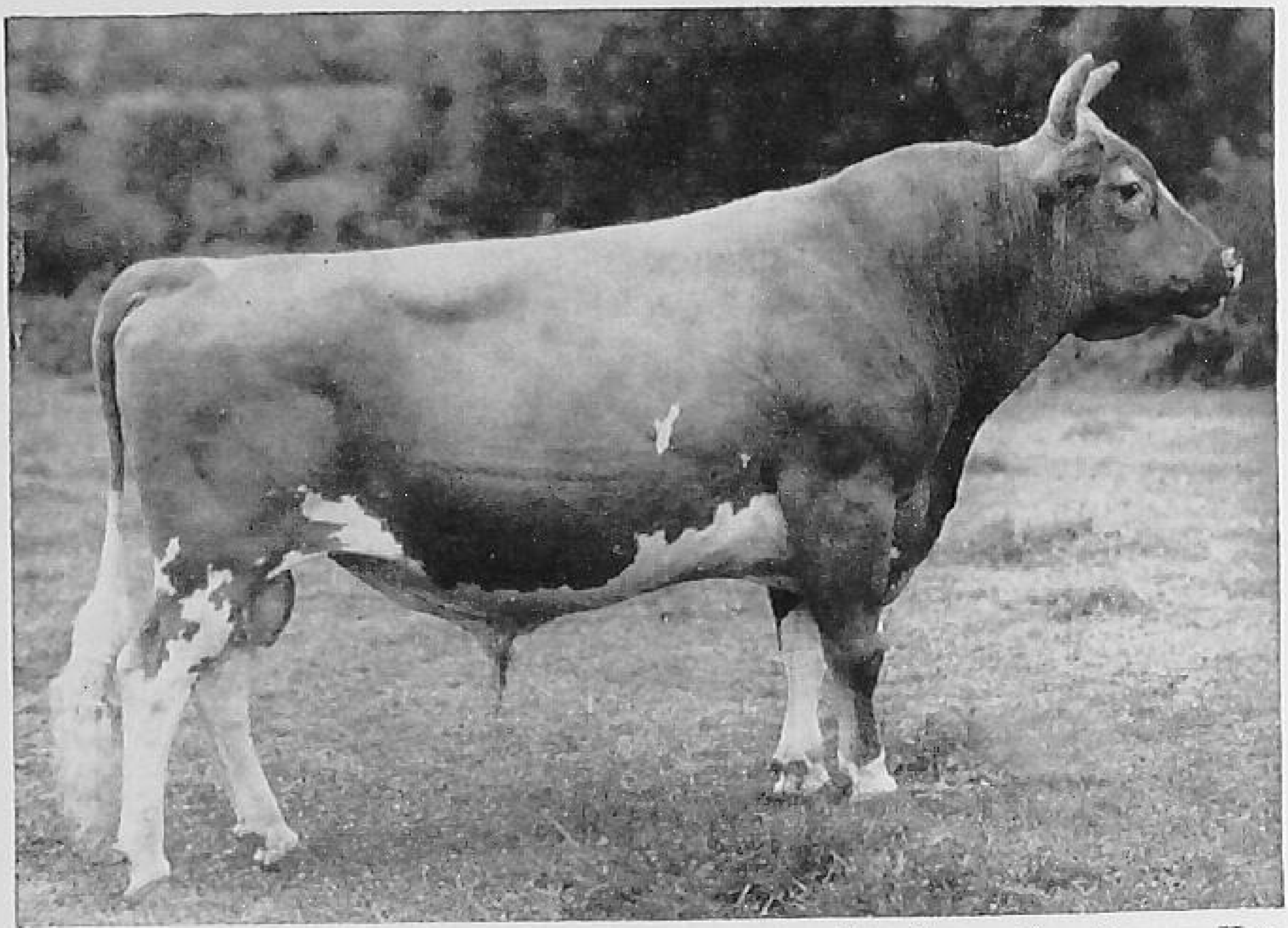

Fig. 222.—The Guernsey bull Foremost Prediction bred by Emmadine Farms, Hopewell Junction, N.Y., owned by McDonald Farms, Cortland, N.Y. (*Photograph Courtesy of Strohmeyer and Carpenter.*)

presumably would still have the sampling feature of inheritance as reduction took place in the formation of the mature egg.

The rapid development of endocrinology has done much to explain the basic principles of growth, reproduction, lactation, egg production, and many other economic characters. The relationships of the genes and hormones are only beginning to be understood. In any complex character such as milk production, it seems logical that nearly every organ system contributes either directly or indirectly to the process. In some cases, for example, the thyroid gland may limit maximum milk production. In this case the administration of the thyroid hormone may have a stimulatory effect. In the same way growth might be limited by the anterior pituitary, thyroid, or gonads. If it were known that the thyroxine secretion of a young animal was suboptimum, the administra-

tion of this hormone might have a stimulatory effect on growth. With an increase in knowledge it may eventually be possible to correct such deficiencies or limiting factors. The cause of such difficulties should not be overlooked. If the deficiency has an environmental cause, much may be gained by its correction. If the deficiency is primarily genetic, there is considerable question as to whether such lines should be propagated. It is evident that in man numerous characters that would be lethal or semilethal under natural conditions are constantly being reproduced. The livestock breeder can practice much more rigid selection than man seems inclined to accept for himself. Deviation from such standards should be given careful thought.

Tremendous strides have been made during the last 50 years in unraveling the heretofore puzzling and seemingly mysterious ways of hereditary transmission. Although the exact nature of genes is still unknown, experimental inquiry has yielded a wealth of information as to the varied nature of their reactions in determining the presence of specific characters. For reasons of expediency and cost, most of these discoveries have occurred in small, rapidly breeding species. Enough work has been done with the larger animals, however, to reveal the very great probability that the genes behave in these animals in approximately the same manner as has been so abundantly proved to be the case in the smaller species. It is true that we do not have for any farm mammal even a beginning of a chromosome map, but this may be no great loss or deprivation, for, as far as the writer knows, the chromosome map of *Zea mays* has not served any utilitarian purpose in the recent remarkable progress in corn breeding.

Work on the chemistry of the gene and the biochemical effects of gene action should provide the animal breeder of the future with powerful working instruments. The fact that in some of the lower forms vitamin and amino-acid synthesis are so closely controlled by specific genes may eventually contribute to the identification of such genes and their functions in higher organisms.

The clear-cut demonstration of the influence of X rays and other radiations on mutations in lower forms and the effects of chemicals, such as mustard gas and colchicine, are shedding new light on the causes of variations. It is not impossible that when the gene, the virus, the enzyme, the hormone, and the vitamin—to mention a few—are understood, and the information integrated, that evolution may be speeded up or molded more to man's purpose. In the past we have had to be content with what nature provided in the way of mutations. Perhaps the time is coming when we can induce beneficial mutations by artificial means and thus speed up the process of animal improvement.

An understanding of the basic principles involved in hereditary transmission gives the modern breeder a compass, with the north, south, east, and west quarters clearly marked, even though it is impossible yet completely to "box the compass."

Animal breeding is still an art, but it is coming to rest more and more securely on scientific foundations. We know that any animal arises from the union of a specific egg and a specific sperm; that the qualities

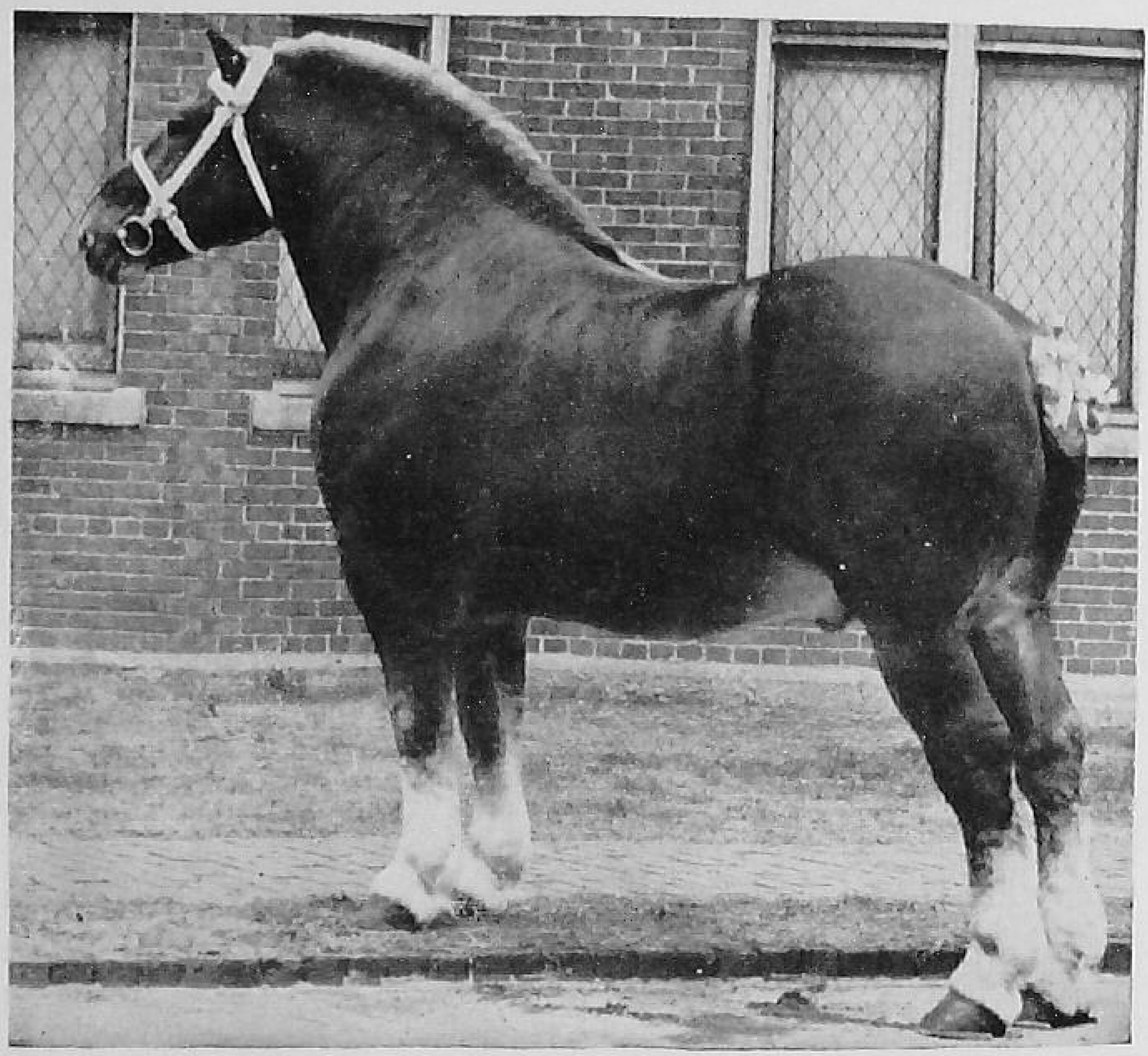

Fig. 223.—Belgian stallion Jay Farceur, grand champion International Livestock Exposition 1938, 1939, and 1940. Bred by J. W. Hillman, Grand Junction, Iowa, owned by H. C. Horneman, Danville, Ill.

of the new individual depend entirely on the genetic make-up of the egg and sperm, regardless of the phase of the moon, direction of the wind, etc., when fertilization takes place; that proper feeding and care of the pregnant female and the offspring after birth are necessary to bring its inherent capabilities to full fruition; that the sorts of germ cells which any animal can produce are determined by the genetic materials supplied it by its parents; that any animal passes on a sample half of its own inheritance, one member of each pair of chromosomes to each of its offspring; that age of itself has no influence on these chance

combinations of hereditary units, *i.e.*, other things being equal, an animal will transmit similarly at one, two, ten, or twenty years of age.

And on the negative side we know that blood does not function in inheritance; that the kind of blood an animal has depends on the genetic content of the egg and sperm which gave rise to it, not vice versa; that acquired characters, telegony, maternal impressions, saturation, and other beliefs of a superstitious age can be consigned to the limbo of the never-was. In inheritance, genes and chromosomes are everything, all else nothing.

It is obvious, therefore, that we will have better livestock only when we have succeeded in so mating our animals that they automatically produce better germ cells, better in terms of containing the genes and gene combinations making for more desirable qualities. Each planned mating which a purebred breeder makes actually covers two generations in the sense that it is designed not only to produce a good immediate offspring but one which will in turn be able to beget better offspring.

There are two major tasks awaiting the livestock industry as a whole. The first is the matter of analysis, or the finding out what we have genetically in our animals as they exist at present. What our livestock will be like 10 or 100 years from now depends on two things: (1) what genes are present in animals now living and (2) our ability to discover the good genes or induce better ones through artificial mutations and to increase their number at the expense of poorer genes.

We[1] have made remarkable progress in animal breeding in the United States since the days of the early settlers. Tough, wiry, streamlined cattle have been largely replaced by blocky, low-set, high-quality bullocks; our sheep have three or four times as much wool spread over a much more desirable carcass; our hogs are more prolific, more efficient, and speedier converters of grass and corn; our horses are heavier and better fitted in every way to relieve the physical burdens of food production; and our dairy cattle produce a greater quantity of a higher quality product than they did in Pilgrim days, in Civil War days, or even in the First and Second World War days. Our methods may have been somewhat of a patchwork of guess, intuition, hocus-pocus, and ballyhoo, but what we had we used in typical, energetic American fashion. Nevertheless, we owe a tremendous debt of gratitude to former generations of breeders for the legacy of genes which through their efforts are now ours. In the march of progress, our breed associations have had a

[1] Most of the material in the next few pages appeared originally as an article by the author entitled Our Breed Associations and was published in the March, 1939, issue of *Successful Farming*. It is reprinted here by permission of the Meredith Publishing Company, Des Moines, Iowa.

prominent part. That they have tended to be a bit conservative is probably a good thing.

A breed association is a group of men banded together for the pedigreeing, protection, and promotion of their particular breed. Most of these associations were organized after the year 1875, making them less than 75 years old at the present time. That they have accomplished great good, no one acquainted with the facts would for one moment doubt.

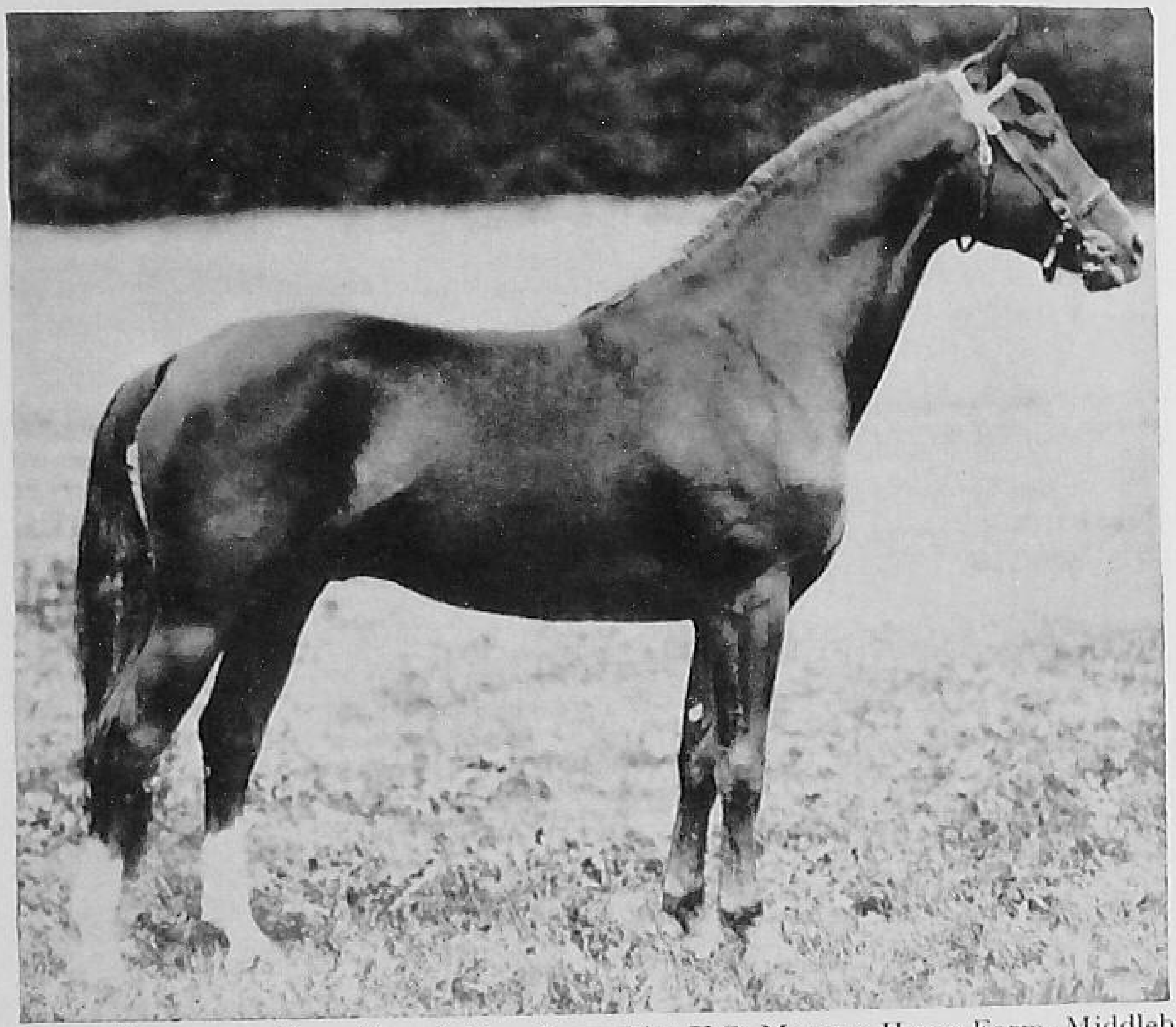

Fig. 224.—Morgan stallion, Mansfield. Owned by U.S. Morgan Horse Farm, Middlebury, Vt.

Like all things human, however, they have had and still have their failings. After 75 years of effort, and because they are recording societies, they should, it would seem, have records to which a breeder could turn for fairly accurate guidance in his job of breeding better livestock. They should now, in other words, be a real help to breeders, because they were organized for that purpose alone and long enough ago for results to have been achieved.

The greatest "lack" in breed associations today is the lack of records of performance. A pedigree that consists merely of names of ancestors without production performance of the ancestors and collaterals is of little value. If, however, the pedigree could be made complete in terms

of records or characteristics, it would be an invaluable guide in the selective mating of animals. For example, if you have brown eyes and your parents, grandparents, great-grandparents, brothers, sisters, cousins, aunts, and uncles all had brown eyes, then we would be reasonably safe in assuming that you would transmit only brown eyes to your children. In livestock, substitute for brown eyes such characteristics as hams, wool characters, loins, rounds, size of litters, efficiency of feed conversion or fattening, etc. Before we can hope for rapid progress in livestock breeding, a way must be found to get records of such performance characteristics on our breeding animals.

The U.S. Department of Agriculture, in cooperation with state colleges of agriculture, inaugurated surveys in 1936 seeking to discover superior breeding animals backed by adequate records. In beef and dual-purpose cattle, the 48 state colleges and experiment stations were able to furnish practically no data that might be useful in locating superior breeding stock. They were asked also to submit the names of breeders who might have such superior stock, and for the whole of the United States 11 stations furnished the names of 64 men—who were not surveyed because of the small likelihood of getting any data of real value. It was the same story in swine, although several stations were carrying on research projects dealing with the inheritance of characters of outstanding economic importance. "Because of the lack of results from the survey of experiment-station herds, contacts with owners of private herds were postponed."

It was the same general story all over again with sheep and horses: no records anywhere to prove breeding worth. In dairy cattle, more tangible results were secured from the state colleges and experiment stations, and the survey extended to dairy-cattle breeders. In all, 1,097 herds were listed, and 708 herds in 40 states were included in the final summary. A total of 4,309 sires in seven breeds were found whose daughters' production could be compared with that of their dams. These bulls were bred to about 30,000 cows whose production averaged 452 lb. of butterfat—the resulting daughters averaged 451 lb. of butterfat. These, remember, are the selected best herds in the country. One farm, after using more than 12 bulls over a 35-year period, ended with approximately the same production it started with.

The first stage of our animal husbandry in America was the introduction and mating of cattle, sheep, swine, and horses by the early settlers. There were no breeds in those early days, just animals. Most of our breeds arose in England, Europe, and America largely during the nineteenth century and largely, be it noted, through inbreeding to intensify desirable characteristics and labels (black for Angus, black and white for

Holsteins, red for Durocs, etc.). Along with this came the formation of breed associations to record pedigrees, to protect the purity of and promote the use of various breeds. Standards of perfection were set up, and the breeds gradually approached the standard by the simple process of weeding out those animals which failed to approximate the breed standards. It was early realized that some animals which were themselves good representatives of the breed lacked the ability to transmit their own desirable qualities. By and large, however, the purebreds were better individuals and better transmitters than grades or scrubs.

This led to the second stage in American animal husbandry, the use of purebred sires for grading up native or grade herds. The demand

FIG. 225.—Grand champion steer, a Hereford, at the 1949 International Livestock Exposition, shown by Pecos County 4H Club, Ft. Stockton, Tex. (*Photograph Courtesy of J. F. Abernathy Livestock Photo Company.*)

for purebreds and the lack of rigid criteria for measuring breeding worth led to the use of many poor purebreds as breeders—to the detriment of animal husbandry in general and the breed in particular. The worst feature of a poor sire from either the breed's or the individual breeder's standpoint is the fact that, if he is used, the harm does not stop with him but breeds on for many generations. The contribution of purebred sires on the whole to our American animal husbandry, though, is beyond calculation. Although some bad sires have been used, the total effect in better loins, rounds, hams, legs, racks, wool, milk, and power is both enormous and well recognized. The breed associations have been great promoters, and they have performed their function in this second stage of animal development with marked success.

The third stage, that of getting more complete and accurate production records so that animals may be proved for breeding value, lies in the

future, and time alone can tell how well the breed associations will respond to this responsibility. Up to the present they have done very little. They have worked hard to preserve the purity of their respective breeds through recording genealogies and also to promote their breeds. True, the dairy breeds have had their AR work for nearly 50 years. Although it represented a considerable advance over the old, recordless days, its value should be apparent after this lapse of time, so that we could now write to a dairy-breed secretary and find out just where we could buy a bull that, when mated to a herd of cows of some known production level, would leave a group of daughters of some certain higher production. This, however, is not yet possible. This does not imply that the secretary would be acting as sales agent for some particular breeder or group of breeders, but rather that the breed had secured facts regarding the transmitting abilities of animals in their respective breeds and had published the facts for breeders and buyers to use as they saw fit. And before we criticize the breed secretary, we should call to mind the fact that he is simply a person hired to carry out the desires of the breeders as expressed through the breed's executive committee or board of directors.

The value of AR work, from a breed-improvement standpoint, has been negligible or worse. Thousands of excellent records have been made and many animals have been sold at long prices because of them, but we know now that an individual's performance and its progeny may be very dissimilar. AR testing is like going into some city, finding the five prettiest girls in the town, and then inducing eligible young bachelors to believe that all the girls in said city are beautiful, and implying probably that they are also good cooks. No, selective testing is not worth the money it costs because it gives a distorted picture of the facts. The poorest bull that ever lived would probably have sired a few good daughters out of really good cows.

The herd test is a lot more satisfactory (records on all animals in a herd year after year), and such testing is now available in all the dairy breeds. Its use should be pushed much harder than is generally being done, and at the same time selective testing should be discouraged. Then, after the records are secured, they should be made readily available to breeders in a form that they can use in selecting breeding stock. The best way is on the basis of a comparison of the daughters' records with those of their dams. Some of the breeds are now doing this.

A fine system of recording D.H.I.A. records and getting valuable data quickly into the hands of the breeder has been set up by the Bureau of Dairy Industry, in cooperation with state colleges. If a bull is being used in a D.H.I.A. herd, we can write to our state extension dairy

specialist and get the breeding facts about the bull as soon as he has five daughters with records from dams with records, as these facts are published several times a year.

From a breed-improvement standpoint the dairy-breed associations could well afford to discourage, and shortly give up entirely, selective testing (as some already have), and try to induce their breeders to test all their cows every year. All the bulls could then be proved while they are still young and vigorous.

The breed associations are now becoming cognizant of their responsibility to provide their members with unselected factual data regarding the animals in their respective breeds. Plans are being developed by many breeds to provide breeders with unselected factual data on which constructive breeding and selection programs can be founded. The plans in the various breeds vary and are being refined as new needs are indicated. Since the plans are in a state of flux (and perhaps always should be), we do not print them herewith but anyone interested can secure them by writing to the breed secretaries as listed in the Appendix.[1] The greatest good can accrue from the breeds securing and publishing records of performance of sires, since the series of sires a breeder uses makes or breaks his herd. If the breeds will do this, fewer mistakes will need to be made by breeders in selecting sires. If, in addition, breeders will study and chart their own female lines, selecting always from the best and letting the poorer lines die out, great impetus will be given to the creation of finer livestock.

Our greatest need is records to prove breeding worth—records as to speed and economy of gains, quality of product, reproductive efficiency, amount and character of wool, longevity, resistance to disease, pulling and staying power, soundness, etc. The job is for each class of stock to set up its own standards and to find practical, economical methods of measuring its animal population against the standards. The purebred breeders, through their associations, should take the lead. It is a challenge that it would seem they cannot ignore.

The other major task awaiting the livestock industry, after that of getting records of performance, is that of fitting together these known ingredients in our animals into strains of animals which will surpass in performance anything that we have known in the past. This is the true art of breeding. In essence, it is merely applying the known principles of reproductive physiology and genetics through systems of breeding and selection in order to attain quickly and surely some preconceived ideal. Selection might be thought of as the anvil and systems of breeding as

[1] The American Dairy Cattle Club (based on production rather than on pureness of pedigree) secretary is Leland W. Lamb, 213 East Seneca St., Ithaca, N.Y.

the hammer. Animals are tested in the fire of record keeping from which the best emerges in a somewhat purified state. Taking this tested material, the breeder with his hammer of breeding system shapes it according to his will against the anvil of selection.

The regional animal-breeding laboratories are carrying on extensive research in inbreeding and outbreeding. Lines are being made relatively homozygous through inbreeding which retain desirable qualities that can be perpetuated in true breeding strains. Crosses between lines are sometimes yielding highly desirable results, and many new strains have been and will continue to be made by outbreeding followed by varying

FIG. 226.—Grand champion wether, a Southdown, at the 1949 International Livestock Exposition, shown by the University of Kentucky. (*Photograph Courtesy of J. F. Abernathy Livestock Photo Company.*)

degrees of inbreeding. Now that the problems of systems of breeding have been attacked on a logical and comprehensive basis, we can confidently look forward to more rapid animal improvement.

The first problem which must be solved we can properly call *analysis*. Its method is that of recording essential data about the performance of our animals, and its success depends largely on our ability to separate the environmental differences from those caused by inheritance, for only the latter are capable of being incorporated into the material passed along from parent to offspring. This second problem we can therefore call that of *synthesis*, the building up of strains of animals that are relatively homozygous for the qualities which make any given class of livestock desirable and profitable.

Up to the present, we have tried to practice this sort of synthesis on the information that we could get by studying individuality and pedigrees

consisting merely of names, with perhaps a modicum of highly selected records to try to make pedigrees look as favorable as possible, extreme care being exercised to keep out any unfavorable data. It is, of course, human to try to put our best foot forward, and a breeder who told the whole truth about his animals would no doubt, temporarily at least, be at a great disadvantage compared with his fellow breeders who were telling only enticing half-truths. Our selection has been based, in other words, on phenotype and made-to-sell pedigrees.

The means of putting a firmer foundation under the whole of our livestock-breeding industry are now at hand. How should we proceed?

1. Study individuality with even greater care and diligence than we have in the past.

2. Get and print relevant breeding and performance data on our breeding animals. In other words, apply the progeny-performance test so that individuality can be more scientifically appraised and pedigrees written which will aid rather than hinder a breeder in arriving at a fair estimate of a young animal's probable performance and transmitting abilities.

3. By systems of breeding render the more desirable strains homozygous by inbreeding or create new strains by outbreeding.

The past 30 or 40 years have furnished the basic scientific principles in terms of reproductive physiology, hereditary transmission, and the control of genital diseases for a sound art of animal breeding. Cooperative efforts among breeders are providing the practical working organizations for putting these scientific discoveries into effect.

Many agencies are now cooperating in livestock-improvement endeavor. The Bureau of Animal Industry "Better Sires—Better Stock" campaign has been instrumental in ridding several whole counties of grade and scrub sires. In many states the extension service working through the county agents is carrying on detailed programs of grading, selection, and culling in all types of livestock, and in some states the college or university is loaning sires to cooperating groups of producers. These projects involve the securing and intelligent appraisal of actual transmitting performances, and many of them involve county and district shows with special attention given to "get-of-sire" classes. In some states county livestock-improvement associations have been formed, and in addition to livestock improvement through the testing of sires and the greater use of proved sires, grading and management demonstrations, and competitive showing, such things as "livestock protective associations" and "cooperative grazing associations" are developing. Such cooperative efforts of producers are in many instances being aided by banks, stockyard companies, railroads, civic clubs, etc.

Regional laboratories for livestock improvement have been established by the Bureau of Animal Industry and the Bureau of Dairy Industry, in addition to the National Agricultural Research Center at Beltsville, Md., to cope with the problem of analyzing our present breeding animals and to devise methods through systems of breeding and selection for rendering them pure in their inheritance for commercially desirable qualities. Last, but by no means least, our breed associations are devising projects aimed at discovering the best in each respective breed and are beginning to foster plans to weed out the poor purebreds.

Constant improvement is being made in the techniques for measuring genetic make-up. Many of these techniques can be used in practical

Fig. 227.—Grand champion barrow, a Berkshire, at the 1949 International Livestock Exposition, shown by Ohio State University. (*Photograph Courtesy of J. F. Abernathy Livestock Photo Company.*)

livestock breeding. In the beef-cattle breeding project at the U.S. Range Livestock Experiment Station and the Montana Agricultural Experiment Station, it has recently been shown that there is a high correlation between the performance of the progeny of proved sires and that of his sibs; between the rate of gain of young bulls and the rate of gain of their progeny, and a high correlation between rate of gain and efficiency of gain. This opens up the possibility of greatly speeding up beef-cattle improvement. In short, rates of gain and weight at fifteen months seem to be highly heritable so that performance of young bulls themselves can be used as a valid selection tool rather than having to wait for performance of their offspring. This short cut over older methods plus the purification of more efficient lines within breeds by inbreeding promise much more rapid improvement in our beef-cattle breeding operations. It is possible that the method can also be adapted to other classes of meat animals.

Some such speeding up is very badly needed in dairy cattle. Possibly solutions will be found in biological analyses of hormone levels on which presumably milk production finally depends.

The two major problems that still confront the breeding and improvement of livestock can be solved only by proving sires and by creating viable and desirable inbred strains to be used either as homozygous "pure lines" or in crosses among themselves, "controlled heterozygosity." The graph shown as Fig. 113 indicates the distribution of 703 indexed Holstein-Friesian bulls. A lot of these bulls are poor, most of them are average, and a few are exceptionally good. In other words, in Holsteins we are generally breeding average bulls to average cows, from which, of course, the only logical expectation is that we will get average offspring. There is no reason to suspect, if we had the breeding data on all the males in use in all the other classes and breeds of livestock, that we would get any different sort of picture.

Since our animal populations in their commercially important features probably simulate a normal curve genetically, the task of the livestock industry is to devise procedures that will reveal the facts about our animals so that those with the better gene complexes may be used in breeding operations and the poorer ones discarded. Since the amount of culling that can be practiced with females is decidedly limited (*i.e.*, we could not overnight dispose of 50 per cent of our dairy cows, desirable as that might be from a genetic standpoint, provided we knew which ones to discard), the problem must be solved largely in terms of males. The procedure both for the industry as a whole and for the individual breeder is obvious. It consists of testing out and proving by means of records of performance of their offspring many times the number of males now being proved. Only in this way can the best males from a genetic standpoint be discovered. When they have thus been discovered, both they and their proved good sons should be used extensively, which probably means the wider adoption of the technique of artificial insemination.

The other major problem is that of carrying on intensive inbreeding experiments on a large enough scale so that they may have a fair chance of being successful. This the individual breeder is generally not equipped to do. The regional animal-breeding laboratories sponsored by the U.S. Department of Agriculture and the individual states are now at work on this problem. If enough strains can be started in closebreeding, a few of them can probably be carried through until they emerge after a few generations as relatively pure strains. Experimental crossing of such strains with the purpose of bolstering the weak points of each can perhaps lead eventually to relatively pure breeding lines in animals, at least in a degree comparable with those already created in plants. There are

many difficulties involved in such a program, but they would not at this time seem to be insurmountable. If such "pure lines" can be created and sires made available to breeders to be used in artificial-breeding associations, or in bull, boar, ram, or stud associations, and if the individual breeder will keep such records as will enable him to select intelligently in his best female lines, animal breeding will begin to approach a scientific level. As pointed out by Dr. Hugh C. McPhee, what we seek in our breeding animals is merit. Genetically, this can be achieved either through homozygosity or perhaps, as in the case of corn breeding, through controlled heterozygosity.

Within the past 20 years a concerted, scientific attack on the problems involved in improving our livestock through breeding has been launched by the Bureau of Animal Industry, and the Bureau of Dairy Industry of the U.S. Department of Agriculture. We are indebted to Dr. Hugh C. McPhee, assistant chief of the Bureau of Animal Industry, for the following discussion of its work:

Regional Swine Breeding Laboratory

The Regional Swine Breeding Laboratory is one of several laboratories established in cooperation with state agricultural experiment stations under authority of the Bankhead-Jones Act of 1935. Each of these regional laboratories was established by the Secretary of Agriculture of the United States at the request of the directors of the state agricultural experiment stations in the region represented. The region covered by the swine breeding laboratory is that of 13 Corn Belt States. A plan setting forth the objectives and procedures was approved by the directors of these experiment stations and officials of the U.S. Department of Agriculture and recommended to the Secretary of Agriculture. The Secretary authorized the establishment of the laboratory in 1937 with headquarters at Ames, Iowa, and assigned it to the Bureau of Animal Industry for administration. The general plan provides for an annual meeting of the technical representatives to formulate and recommend the program of research to be pursued.

Objectives.—The primary objectives of the laboratory are (1) to discover, develop and test procedures of breeding and selection which may aid hog producers in improving hogs in respect to performance and carcass, (2) to investigate precisely the use of inbred lines for improving the breeding value of pure breeds and for use in pork production, (3) to enlarge knowledge concerning the genetic effects of inbreeding and inheritance of characters in swine, and (4) to evaluate and demonstrate application of such knowledge in swine breeding.

Procedures.—The general procedures for the research undertaken in the various projects up to the present time relate to devising and testing methods of selection, developing and using inbred lines in various types of crosses, determining the consequences of inbreeding swine, evaluating the carcass desirability of various lines and crosses, determining the heritability of performance characters, and some of the physiological aspects of the breeding performance of sows and boars.

Three systems of breeding have been followed:

1. Inbreeding for the purpose of establishing inbred lines to permit converging in single and double crosses within lines and topcrossing of inbred boars on noninbred sows. Three intensities were used: four-sire, two-sire, and one-sire closed herds.

2. Selection based entirely on rate of growth in a herd closed to outside blood in which the inbreeding is kept at a negligibly low level.

3. Selection in a herd started from crossing 2 established breeds and subsequently closed to outside bloods, selections being based on performance and carcass merit.

Regional Beef Cattle Breeding Program

The Bureau of Animal Industry is conducting an extensive beef cattle breeding program in cooperation with the state agricultural experiment stations in the western, north-central, and southern regions of the United States. This program differs in several respects from the regional breeding laboratories established under authority of the Bankhead-Jones Act. The financial support comes from the Research and Marketing Act of 1946. There is a regional experiment station advisor and a technical committee for each region to advise with the national coordinator on matters pertaining to initiation of projects, procedures and allocation of funds. The national coordinator is also in charge of other beef cattle research for the Bureau of Animal Industry and at present has headquarters at Denver, Colorado.

Objective.—To improve beef cattle production with respect to quality and efficiency through use of sib tests in predicting breeding value of lines and combinations of lines of beef cattle and through propagation and distribution of superior lines and combinations.

Procedures.—Utilizing available basic research information on how to develop better lines and how to measure genetic variability this new program will test, synthesize, and put to use in the field new lines of superior beef cattle. State experiment station and privately-owned unrelated herds of Hereford, Angus, Shorthorn, and other pure breeds of cattle and lines derived from combinations of lines of these breeds will be sib tested. Superior lines and combinations of lines will be propagated and distributed through cooperating state experiment stations to beef cattle producers for further testing under field conditions.

Western Sheep Breeding Laboratory

This regional laboratory was established in 1937 by the Secretary of Agriculture acting upon a request of the experiment station directors in the 12 far-western states, including Texas. The headquarters were placed at the U.S. Sheep Experiment Station, Dubois, Idaho, at the request of the station directors for the reason that the Bureau of Animal Industry already had available at that point a large physical plant consisting of buildings and sufficient land for spring, summer, fall and winter range for a large number of sheep. No experiment station in the

region was similarly equipped to maintain the number of animals required by the proposed research program.

The laboratory is assigned to the Bureau of Animal Industry for administration and is in charge of a director, who is also in charge of the program of the U.S. Sheep Experiment Station carried on at the same location. These two programs are separate and distinct in regard to budget and animals, but are fully coordinated by the director and his staff. In the beginning the program of the Western Sheep Breeding Laboratory was limited to the Rambouillet breed. The program of the U.S. Sheep Experiment Station includes breeds other than the Rambouillet, principally Columbia and Targhee. It also embraces other lines of research such as range sheep management, sheep feeding, and range vegetation.

An annual meeting of technical representatives of the cooperating state experiment stations is scheduled, at which time the research progress is reviewed and plans are adjusted for the coming year. Between such meetings the director visits the cooperating experiment stations and reviews current projects which are being conducted as part of the over-all program.

Objective.—The main objective is to improve Rambouillet sheep for lamb and wool production under range conditions.

Procedures.—To attain this objective, basic breeding methods are employed, heritability analyses are made of the various utility factors and selection is based on production as it is measured under range conditions. Emphasis is placed primarily on the quantity and quality of lambs produced; the length, quality, and quantity of clean scoured wool and upon the adaptability and longevity of the sheep.

Development of systems of breeding for locating strains of Rambouillet sheep which may possess combinations of genes that will improve strains with which they may be crossed includes:

1. The development of inbred strains or lines by mating animals as closely related as possible with emphasis on selection for all characters of economic importance.

2. The development of inbred lines with special reference to very important characters that are of economic significance in range sheep such as mutton form, length of staple and open faces.

3. The development of non-inbred control groups.

For the purpose of developing methods by which undesirable characteristics can be eliminated from Rambouillet sheep, the inheritance of abnormalities in the growth of wool, hairiness in the fleece and skin folds as wrinkles are being studied. Supporting projects in physiology of reproduction are also being carried on with special reference to sexual maturity of ram lambs, quality of semen in relation to fertility and factors affecting fertility of ewes.

The Bureau of Dairy Industry has made some notable contributions to better breeding through continued use of proved sires, having raised butterfat production in their Holstein and Jersey herds by about 200 lb. per year. This bureau has also contributed much to our knowledge of inbreeding and is now embarked on a program of crossbreeding.

Not so many years ago animal breeding was thought by many to involve a considerable amount of magic, which could be invoked by only a select few on the basis of a God-given instinct. Genetics has dispelled this myth and made it evident that anyone who is willing to take the pains to analyze his animals in terms of their producing and transmitting abilities can also use, with varying degrees of success to be sure, the only tools which ever have been or will be available for animal improvement—breeding systems and selection.

A proton and electrons, then elements emerge—
They organize and synthesize to form a living surge.
Then animals and man appear in orderly progression:
Teamed, they move with quickened pace—a fitting, joint possession.

APPENDIX

Livestock Record Associations

The following list of livestock record associations, as of Sept. 1, 1950, is presented through the courtesy of Mr. H. J. Brant, secretary of the National Society of Livestock Record Associations with headquarters at 282 South Wabash Street, Wabash, Ind. This society was organized in 1911 and represents over 350,000 breeders of purebred livestock. The purposes of the society are stated as follows:

"The objects of this Society shall be to advance the interests of member registry associations, (1) by devising and perfecting methods for preserving pedigrees of purebred animals; (2) by endeavoring to secure the enactment of equitable laws relating to the purebred livestock industry and to livestock record associations; (3) by securing the adoption of just freight and express rates on exhibition and breeding stock; and (4) by originating or participating in any and all other activities which will in the judgment of the Directors of the Society advance the interests of breeders of purebred livestock through their respective registry associations."

Beef and Dual-purpose Cattle

American Aberdeen-Angus Breeders Association, Union Stock Yards, Chicago 9, Ill., Frank Richards, Secretary.
American Brahman Breeders' Association, 2711 South Main Street, Houston 2, Tex., Mrs. G. R. Sunday, Secretary.
American Devon Cattle Club, Inc., Meredith, N.H., W. J. Neal, Secretary.
American Galloway Breeders' Association, Henry, Ill., Rank C. Forbes, Secretary.
American Hereford Association, 300 West 11th Street, Kansas City, Mo., Jack Turner, Secretary.
American Kerry and Dexter Club, Independence, Iowa, Roy Cook, Secretary.
American Polled Hereford Breeders' Association, 1110 Grand Avenue, Kansas City 6, Mo., Don Chittenden, Secretary.
American Polled Shorthorn Society, Union Stock Yards, Chicago 9, Ill., C. D. Swaffer, Secretary.
American Red Danish Cattle Association, Fairview, Mich., Clifford Shantz, Secretary.
American Scotch Highland Breeders' Association, Henry, Ill., Rank C. Forbes, Secretary.
American Shorthorn Breeders' Association, Union Stock Yards, Chicago, Ill., Clinton K. Tomson, Secretary.
Red Polled Cattle Club of America, 3275 Holdredge Street, Lincoln, 3, Nebr., F. A. Sloan, Secretary.
The American Milking Shorthorn Society, 4122 South Union Avenue, Chicago 9, Ill., W. J. Hardy, Secretary.

Dairy Cattle

American Guernsey Cattle Club, Peterborough, N.H., Karl B. Musser, Secretary.
American Jersey Cattle Club, Sixth and Long, Columbus 15, Ohio, Floyd Johnston, Secretary.

Ayrshire Breeders' Association, Brandon, Vt., C. T. Conklin, Secretary.

Brown-Swiss Cattle Breeders' Association, Beloit, Wis., Fred S. Idtse, Secretary.

Dutch Belted Cattle Association of America, Anamosa, Iowa, Thomas Stimpson, Secretary.

Holstein-Friesian Association of America, Brattleboro, Vt., H. W. Norton, Jr., Secretary.

Draft Horses

American Clydesdale Association, Union Stock Yards, Chicago 9, Ill., Miss Margaret Coridan, Secretary.

American Shire Horse Association, 319 East 4th Street, Des Moines, Iowa, E. F. Fox, Secretary.

American Suffolk Horse Association, Clinton, N.J., L. B. Wescott, Secretary.

Belgian Draft Horse Corporation of America, Wabash, Ind., H. J. Brant, Secretary.

Percheron Horse Association of America, 809 Exchange Avenue, Union Stock Yards, Chicago 9, Ill., Mrs. Anne Brown, Secretary.

Light Horses

American Albino Horse Club, Inc., Butte, Neb., Ruth Thompson, Secretary.

American Hackney Horse Society, Room 1737, 42 Broadway, New York, N.Y., Mrs. J. Macy Willets, Secretary.

American Quarter Horse Association, 1405-b West 10th Avenue, Amarillo, Tex., Raymond D. Hollingworth, Secretary.

American Saddle Horse Breeders' Association, 929 South Fourth Street, Louisville, Ky., C. J. Cronan, Jr., Secretary.

Appaloosa Horse Club, Moscow, Idaho, George B. Hatley, Secretary.

Arabian Horse Club of America, 111 West Monroe Street, Chicago 3, Ill., Frank Watt, Secretary.

Cleveland Bay Society, White Post, Va., A. Mackay Smith, Secretary.

Morocco Spotted Horse Association of America, Greenfield, Iowa, LeRoy Fritz, Secretary.

National Quarter Horse Breeders' Association, Houston 5, Tex., J. M. Huffington, Secretary.

Palomino Horse Association, Reseda, Calif., Jim Fagan, Secretary.

Palomino Horse Breeders of America, Mineral Wells, Tex., Dr. H. Arthur Zappe, Secretary.

Pinto Horse Society, Concord, Calif., George M. Glendenning, Secretary.

Tennessee Walking Horse Breeders' Association of America, Lewisburg, Tenn., Miss Syd Houston, Secretary.

The Jockey Club (Thoroughbred), 250 Park Avenue, New York 17, N.Y., Marshall Cassidy, Secretary.

The Morgan Horse Club, 90 Broad Street, New York 4, N.Y., F. B. Hills, Secretary.

United States Trotting Association (Standardbred), Goshen, N.Y., Neil R. Gahan, Secretary.

Ponies

American Shetland Pony Club, P.O. Box. 2557, South Bend, Ind., Wayne C. Kirk, Secretary.

Welsh Pony Society of America, 417 West Engineering Bldg., University of Michigan, Ann Arbor, Mich., Frank H. Smith, Secretary.

Jacks and Jennets

Standard Jack and Jennet Registry of America, P.O. Box 375, Garden City, Kan., Mrs. N. E. Hineman, Secretary.

Sheep

American Cheviot Sheep Society, Oneonta, N.Y., Mrs. Katherine S. Turrell, Secretary.

American Corriedale Association, 100 North Garth Street, Columbia, Mo., Rollo E. Singleton, Secretary.

American Cotswold Registry Association, Union Stock Yards, Chicago 9, Ill., F. W. Harding, Secretary.

American and Delaine-Merino Association, Marysville, Ohio, Walter M. Staley, Jr., Secretary.

American Hampshire Sheep Association, 72 Woodland Avenue, Detroit 2, Mich., Mrs. Helen Tyler Belote, Secretary.

American Oxford Down Record Association, Clayton, Ind., J. M. McHaffie, Secretary.

American Rambouillet Sheep Breeders' Association, San Angelo, Tex., Geneva Caldwell, Secretary.

American Romney Breeders' Association, 200 Dairy Building, Corvallis, Ore., H. A. Lindgren, Secretary.

American Shropshire Registry Association, Lafayette, Ind., Chas. F. Osborn, Secretary.

American Southdown Breeders' Association, 212 South Allen Street, State College, Pa., William L. Henning, Secretary.

American Suffolk Sheep Society, Moscow, Idaho, C. W. Hickman, Secretary.

Black Top and National Delaine-Merino Sheep Breeders' Association, Houston, Pa., I. Y. Hamilton, Secretary.

Columbia Sheep Breeders' Association of America, Box 2466, State College Station, Fargo, N.D., M. L. Buchanan, Secretary.

Continental Dorset Club, Hickory, Pa., J. R. Henderson, Secretary.

Karakul Fur Sheep Registry, Friendship, Wis., L. K. Brown, Secretary.

Montadale Sheep Breeders' Association, 61 Angelica Street, St. Louis, Mo., E. H. Mattingly, Secretary.

National Lincoln Sheep Breeders' Association, College Manor, Apartment 10, East Lansing, Mich., Harry Crandell, Jr., Secretary.

National Suffolk Sheep Association, Middleville, Mich., C. A. Williams, Secretary.

National Tunis Sheep Registry, Fulton, N.Y., Ralph E. Owen, Secretary.

Texas Delaine-Merino Record Association, Brady, Tex., George H. Johanson, Secretary.

Goats

American Angora Goat Breeders' Association, Rocksprings, Tex., Mrs. Thomas L. Taylor, Secretary.

American Goat Society, Inc., Mena, Ark, R. D. Weis, Secretary.

American Milk Goat Record Association, Sherborn, Mass., Miss Mary L. Farley, Secretary.

Swine

American Berkshire Association, 410 South 5th Street, Springfield, Ill., Noel F. Titus, Secretary.

American Essex Swine Association, 1335 East 2d Street, Muscatine, Iowa, Mrs. J. J. Lighthall, Secretary.

American Spotted Poland-China Association, Moberly, Mo., Van G. Sutliff, Secretary.

American Yorkshire Club, Wallace Building, LaFayette, Ind., Bob Shannon, Secretary.

Breeders Chester White Record Association, 330 Royal Union Building, Des Moines 9, Iowa, L. W. Drennen, Secretary.

Chester White Record Association, Rochester, Ind., Levi P. Moore, Secretary.

Hampshire Swine Registry, Commercial National Bank Building, Peoria, Ill., R. L. Pemberton, Secretary.

Kentucky Red Berkshire Swine Association, Lancaster, Ky., Hogan Teater, Secretary.

National Hereford Hog Record Association, Chariton, Iowa, Harris Sellers, Jr., Secretary.

National Mule Foot Hog Association, DeGraff, Ohio, O. C. Kreglow, Secretary.

National Spotted Poland-China Record Association, 3153 Kenwood Avenue, Indianapolis 8, Ind., Fred L. Obenchain, Secretary.

O.I.C. Swine Association, Brookville, Ohio, Mrs. Jane Roper, Secretary.

O.I.C. Swine Breeders' Association, Goshen, Ind., Harry C. Miller, Secretary.

The Poland-China Record Association, Galesburg, Ill., C. G. McCahan, Secretary.

Tamworth Swine Association, Hagerstown, Ind., R. H. Waltz, Secretary.

United Duroc Record Association, Peoria 3, Ill., B. R. Evans, Secretary.

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